NATURAL DISTURBANCE AT THE SITE AND LANDSCAPE LEVELS IN TEMPERATE RAINFORESTS OF SOUTHEAST ALASKA

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ABSTRACT

Wind disturbance in forests of southeast Alaska is poorly understood. Dynamics of canopy gaps, formed primarily by wind, were investigated in the western hemlock (*Tsuga heterophylla*)/blueberry (*Vaccinium spp.*)/shield fern (*Dryopteris austriaca*) plant association in northern southeast Alaska; twenty gaps were sampled at each of 3 sites. Gaps comprised about 9% of the forest area. The majority of gaps were < 50 m^2 in area, had a diameter-to-height (D/H) ratio < 0.50, were created from the death of 1 or 2 gapmakers, and had experienced gap expansion. Emulating the small-scale natural disturbance regime would be best achieved if single tree selection and small group selection cuts were administered within a stand.

Diffuse light levels were greatest and most variable at both the shrub and herb layers in canopy gaps, and lowest and least variable under closed canopy forest. Shrub layer light levels were positively associated with mean and median canopy gap areas. Herb layer light levels, however, were determined by the amount of light interception at the shrub layer and not by canopy gap size.

Most species were robust in terms of their light requirements compared to the range of light conditions present in the understory. Sorenson Index values indicated that gaps and closed canopy forest generally were very similar in species composition. Seedling heights suggest that western hemlock and Sitka spruce seedlings benefit from the presence of canopy gaps. However, the ability of Sitka spruce to maintain itself through gap-phase replacement is limited.

Techniques are needed that allow forest managers to interpret wind patterns in remote locations, at both site- and landscape-levels, and across complex topography. I demonstrated the use of circular data analysis of treefall directions as a technique to investigate wind flows at the site-level. I also demonstrated the feasibility of mapping wind flows across a large landscape of complex terrain in southeast Alaska using flagged trees, treefall directions of large-scale natural blowdowns, and treefall directions of blowdowns associated with clearcuts.

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CHAPTER 1
INTRODUCTION TO NATURAL DISTURBANCE CONCEPTS AND THIS RESEARCH PROJECT

HISTORICAL DEVELOPMENTS OF IDEAS RELATING TO THE IMPORTANCE OF NATURAL DISTURBANCE

American plant ecologists have debated the role of natural disturbance in natural ecosystems for most of this century. Prior to the early 1970s most ecologists supported the succession-to-climax paradigm (Sprugel 1991) in which developing natural communities advanced along a pathway of predictable seres until a climax community was attained. The climax community was believed to be in an equilibrium condition as a result of autogenesis within a stable environment.

Natural disturbances were viewed as major, exogenous events causing abrupt changes in community structure (White 1979) that moved communities away from the equilibrium state. Examples of these disturbances were floods, fires, avalanches, lava flows, hurricanes, tornadoes, and other large windstorms. Problems with this traditional view of natural disturbance were:

1) The change caused by a particular disturbance agent varies from negligible to extreme, depending on the intensity of the disturbance agent and the susceptibility of the organisms (White 1979, Sousa 1984);

2) Biotic components of a community can initiate and promote disturbance (White 1979) (e.g. fungal infections can pre-dispose trees to wind damage); and

3) Few natural communities or populations remain at or near equilibrium conditions on a local scale (Connell and Sousa 1983).

Wide-spread recognition of the importance of natural disturbance came about in the early 1970s (Sprugel 1991) as evidenced by numerous examples of papers that espoused the importance of natural disturbance in western conifer forests (e.g. Habeck and Mutch 1973, Kilgore 1973), eastern conifer forests (e.g. Sprugel 1976, Reiners and Lang 1979), northern boreal forests (e.g. Rowe and Scotter 1973, Viereck 1973), deciduous forests (e.g. Loucks 1970, Bormann and Likens 1979), chaparral (e.g. Hanes 1971, Biswell 1974), rocky intertidal zones (e.g. Dayton 1971), and other ecosystems (White 1979).

Natural communities are now recognized as being dynamic and spatially and temporally heterogeneous. Disturbance is known to be a major cause of spatial and temporal heterogeneity in community structure and dynamics and a factor of natural selection in the evolution of life histories (Sousa 1984). Some of these ideas are reflected in contemporary (post-1970s) definitions of disturbance such as:

> a discrete, punctuated killing, displacement, or damaging of one or more individuals (or colonies) that directly or indirectly creates an opportunity for new individuals (or colonies) to become established (Sousa 1984),

and

> any relatively discrete event in time that disrupts ecosystem, community, or population structure and changes resources, substrate availability, or the physical environment (White and Pickett 1985).

Contemporary views of natural disturbance recognize the various spatial and temporal scales at which these events operate, the less than abrupt nature of some disturbances, and biotic disturbance agents. Also, some natural disturbance events cannot be easily attributed to strictly an exogenous or endogenous agent. For example, some trees killed by a windstorm may be pre-disposed to wind damage because of weakened structural support caused by fungal infection, while other trees may be healthy and solid yet still succumb to the same windstorm. The degree to which a disturbance is a result of exogenous or endogenous factors can vary considerably, just as the amount of change caused by a particular disturbance agent can vary along a continuum from negligible to extreme.

Definitions of natural disturbances now include large-scale abrupt events, some of which have already been mentioned, as well as smaller-scale exogenous events, endogenous events, and biotic as well as abiotic events such as:

1) Ice storms—These disturbances are caused by exogenous factors that influence natural communities at a variety of scales.

2) Small-scale gap formation in plant canopies—Gaps are formed in plant canopies of communities such as grasslands and forests when a portion of a plant, or one or several dominant or codominant individuals die. Plant death can result from biotic or abiotic causes; it can be abrupt or gradual.

3) Animal browsing and burrowing, insect damage, and fungal damage—These disturbances are caused by biotic agents that occur at a variety of scales.

Besides recognizing disturbances as an inherent part of ecosystems, current views seem to favor the existence of nonequilibrium ecosystems (Rogers 1996). Sprugel

(1991) suggested 3 conditions that may result in nonequilibrium landscapes. First, a nonequilibrium landscape can occur where the spatial scale of disturbance is very large, approaching or exceeding a typical landscape unit. Examples are the forests of the Pacific Northwest where fires have occurred on the scale of hundreds of thousands of hectares (Franklin and Hemstrom 1981), and spruce-fir forests of eastern North America where spruce budworm (*Choristoneura fumiferana*) outbreaks have occurred over millions of hectares (Hardy 1985). Where disturbances of such magnitude occur, the proportion of the landscape in different developmental stages will shift widely from one decade or century to the next, making equilibrium unlikely (Sprugel 1991).

Second, a nonequilibrium landscape can occur where a unique disturbance event has long-lasting effects on an area. For example, the landscape in the vicinity of Mount St. Helens in Washington State will be responding to the 1980 eruption of the volcano for centuries to come.

Third, climatic changes can cause shifts in vegetation distribution and abundance large enough to prevent landscapes from achieving equilibrium. Climatic variations are the principal source of variability in the environment of plants (Bartlein 1988). Variations in climate occur at all spatial and temporal scales. Decadal and century long climatic anomalies (e.g. Little Ice Age) result in vegetation responses such as succession, abundance changes, and limited changes in vegetation distribution. In southeast Alaska, for example, the frequency of snow avalanches has declined since the late 1970s in response to climatic warming. The result is that mountain hemlock (*Tsuga mertensiana*) is colonizing alpine tundra in the region (Veblen and Alaback 1996). Climatic variations on the scale of thousands and tens of thousands of years result in wholesale range and abundance changes (Bartlein 1988). Sitka spruce (*Picea*

sitchensis), for example, is still expanding its range westward into Alaska in response to a warming trend that has been occurring since the last major ice advance (Veblen and Alaback 1996). With vegetation responding to climatic variation at several scales simultaneously, it is reasonable to assume that landscapes are more likely to be in a nonequilibrium condition rather than in equilibrium.

Although current thought prefers nonequilibrium to equilibrium landscapes, the concept of natural disturbance regimes implies that disturbances of natural communities, ecosystems, or landscapes exhibit a central tendency or predictability. This implicit assumption is reflected in descriptors of natural disturbance regimes such as rotation periods and return intervals described below.

NATURAL DISTURBANCE REGIMES OF FORESTS AND THEIR DESCRIPTION

Disturbance regimes of forests can be characterized by the mortality patterns of trees in the dominant canopy layer (Runkle 1985). Traditionally, forest dynamics research has been directed at large-scale disturbances created by agents such as flooding, landslides, and fire (White 1979), with emphasis primarily on the process and stages of plant succession (Lorimer 1985). More recently, the role of small-scale disturbances ranging from the death of a large branch up to the death of several trees has been studied in numerous forest systems (e.g. Barden 1981, Runkle and Yetter 1987, Stewart et al. 1991).

Regardless of scale, disturbance regimes can be characterized with the following descriptors (White and Pickett 1985):

1) Spatial distribution;

2) Frequency—average number of events per time period;

3) Return interval—average time between disturbances;

4) Rotation period—average time required to disturb the area of interest;

5) Predictability—scaled inverse function of variance in the return interval;

6) Area disturbed—area per time period, per event, per event per time period, or total area per disturbance type per time period;

7) Magnitude:

a) Intensity—strength of the disturbing force (e.g. wind speed, fire temperature),

b) Severity—impact or damage of the disturbing force on the organism, community, ecosystem, or landscape;

8) Synergism—effects on the incidence of other disturbances (e.g. weakening of trees by fungal infections increases susceptibility to wind damage).

SMALL-SCALE NATURAL DISTURBANCE REGIMES

Small-scale forest disturbance results when death of part of a tree or death of one or several trees forms an opening or "gap" in a forest canopy. Typically, disturbances of this nature are described only if they occur in the dominant and codominant canopy layers.

Gaps occur in the old-growth stage of forest development described by Oliver (1981). According to Oliver's model, a forest that is initiated following a large-scale disturbance goes through 4 stages of development in the absence of additional major disturbances:

1) The stand initiation stage represents the time during which new seedlings actively invade a site, and sprouting stems and advance regeneration begin or resume growth.

2) The stem exclusion stage represents the time during which new stems are excluded from initiating and vertical stratification by species occurs in the existing stems because of intense competition for resources. The stem exclusion stage usually begins upon canopy closure in light-limited forests.

3) The understory reinitiation stage is the period when herbaceous and woody plants, including advance regeneration, begin to grow in the understory as the overstory becomes very mature.

4) The old growth stage is the final stage of development when the overstory slowly breaks up (i.e. gaps are formed) and understory advance regeneration is locally released and moves into the overstory canopy.

"The gap paradigm is formulated as a gap vs. non-gap dichotomy of forests" (Lieberman et al. 1989). The conceptualization of a forest as either gaps or non-gaps has resulted in criticism of the gap paradigm because it over-simplifies forest complexity. Lieberman et al. (1989) argued that gap studies are flawed by circular reasoning because the classification of forests into gaps and non-gaps is tested by comparing variables or species of interest that are first dichotomized as being associated with a gap or non-gap area. Other problems of gap studies are that "gaps are statistically intransigent because their precise measurement is almost impossible, they are patchily distributed in time and space, they have highly skewed frequency distributions, and they change through time" (Ogden et al. 1991). Also, the methodologies used in gap studies are only appropriate for relatively closed-canopy

forests where gaps can be defined. For example, canopy gaps can not be defined in some of the riparian forests of southeast Alaska or spruce forests of interior Alaska (pers. observ.). Lieberman et al. (1989) suggested that the sampling units be shifted from gaps and non-gaps to individual trees, and that research should be focused on light level gradients or canopy closure. However, tree death simultaneously influences numerous resources such as light, water, nutrients, and physical space. Forest response to disturbance integrates changes along all resource gradients. Publicover and Vogt (1991) pointed out that measuring competition for water or nutrients using a tree-centered variable, similar to the canopy closure index for light suggested by Lieberman et al. (1989), would be difficult because of interactions of tree root systems through grafting and intermingling. Publicover and Vogt (1991) also noted that the formation of belowground gaps may be more important than canopy gaps in forests that are nutrient- or moisture-limited instead of light-limited. For these reasons, using gaps as sample units has merit. Also, even with the problems of gap studies, parameters such as proportion of land area in gaps and average return time of gaps are valuable comparative indices of forest dynamics (Ogden et al. 1991).

IMPORTANCE OF UNDERSTANDING NATURAL DISTURBANCE REGIMES OF FORESTS

Ecological Importance

From an ecological perspective, understanding natural disturbance regimes contributes to 1) our understanding of dynamics within a forest of interest, and 2) how and why different forest types vary with regard to structure and function. Tree

death is an important ecological process that brings about changes in forest structure and function such as (Franklin et al. 1987):

1) Alterations of tree population structures;

2) Alterations in community structure;

3) A shift from biomass to necromass;

4) Release of resources such as light, nutrients, moisture, and physical space;

5) Storage of resources by decomposers;

6) Creation of new resources such as snags, logs, and complex organic compounds; and

7) Work such as soil mixing by uprooting is carried out.

The scales and spatial and temporal patterns of tree mortality also influence the relative importance of ecological changes brought about by tree death. Large- and small-scale disturbances mark the endpoints of a disturbance continuum.

Additionally, natural disturbance regimes are hypothesized to play a role in the evolution of organisms (White 1979, Sousa 1984). Numerous plant species, for example, are known to be dependent upon forest canopy gaps (e.g. Watt 1923, Bray 1956, Williamson 1975, Fox 1977). Denslow (1980) suggested that life history strategies of disturbance-dependent plant species should be related to the size-frequency distribution of disturbances within the community in which they exist, thereby resulting in the most common plant species in a community being those that are adapted to establishment and growth in the most common patch types.

Understanding specific effects of natural disturbance on a forest system requires knowledge of the disturbance regime as well as knowledge of the response of the forest to the disturbance regime. For example, instantaneous tree death may

influence forest structure and function differently than gradual tree death because resources utilized by a tree prior to death would presumably be freed more gradually in the case of gradual tree death (Krasny and Whitmore 1992, Franklin et al. 1987).

Thorough discussions regarding the role of disturbance in communities and ecosystems, and ecosystem response to disturbance can be found in White (1979), Sousa (1984), Pickett and White (1985), and Attiwill (1994b).

Management Importance

Natural resource management has evolved from regulation of uses where the focus was on avoidance of obviously undesirable uses, to sustained yield management where the focus was on a few desirable products, to sustainable ecosystem management where the focus is on the health of the ecosystem which provides numerous goods and services (Salwasser 1990). The concept of management of entire ecosystems and landscapes has been termed "ecosystem management." Salwasser and Pfister (1994) defined ecosystem management as:

> the process of seeking to produce (i.e., restore, sustain, or enhance) desired conditions, uses, and values of complex communities of organisms that work together with their environments as integrated units.

Society's expectations and demands concerning how our natural resources should be managed have expanded in recent times; resource management practices have not kept pace with these demands. Sustainable ecosystem management is intended to better match management practices with this broader array of society's philosophies and values regarding natural resource management (Swanson and Franklin 1992).

Resource management professionals "now are being asked to manage not just for traditional products such as timber, water, game animals and fish, recreation, and minerals but also for complex ecological values, esthetics, and issues of global concern" (Szaro 1992). The challenge to natural resource managers will be to maintain or even increase the level of natural ecosystem processes (e.g. diversity, resilience, productivity) and interactions within and among ecosystems while still supplying tangible goods and services demanded by society.

In the case of forests, Attiwill (1994b) concluded that management of natural forests should be based upon an understanding of the ecological processes of natural disturbance because diversity, structure, and function of forests are shaped by these events. Ecosystem processes, however, are often difficult to measure and manage directly. Typically, ecological research and management activities operate under the "pattern-process paradigm" which Urban (1994, page 128) summarized as follows: "*Ecological processes generate patterns, and by studying these patterns we can make useful inferences about the underlying processes.*"

An implicit working hypothesis in ecosystem management based upon the "pattern-process paradigm" is that saving the pattern in an ecosystem or landscape will save the processes as well (Urban 1994). It seems reasonable to assume that forest ecosystem management will be based upon this paradigm, at least in the foreseeable future. Therefore, understanding natural disturbance regimes is important for forest management because of the link between tree death and ecological processes outlined by Franklin et al. (1987) and summarized above.

Knowledge of the historical variability of ecosystem structure and function, along with knowledge of the natural disturbance regimes that influence that variability, is

being used to design ecosystem management systems (Swanson et al. 1994) and to determine if current management systems can be contained within the parameters of natural disturbance (e.g. Attiwill 1994a). For example, understanding small-scale natural gap dynamics may provide a foundation for sustained management of uneven-aged, mixed species stands on commodity production lands (Denslow and Spies 1990). Part of the rationale for this approach is the idea that organisms have evolved in response to historical habitat and disturbance conditions (White 1979, Denslow 1980, Sousa 1984) as already discussed. Management activities that deviate from those historic conditions may result in loss of species and undesirable ecological changes (Swanson et al. 1994).

Ecosystem management of forested landscapes may involve setting aside some forest lands, especially old-growth forests, for the purposes of maintaining species diversity and ecosystem processes unique to these forests. Also, forest managers will want to maintain or enhance structural characteristics of old-growth forests in actively managed forests. However, controversy exists as to what constitutes an old-growth forest. Generally, old-growth forests are defined in terms of structural characteristics based upon current stand structure such as: large, live old trees; large snags; large logs on land; and large logs in streams (Franklin et al. 1981). However, Samson et al. (1989) suggested that areal extent is a key element of an ecological definition of old-growth forest, because sufficient stand size is important for preserving interior forest dynamics—such as natural disturbance processes—as well as maintaining microclimate characteristic of old-growth forests, and ensuring long-term survival of these stands. Therefore, understanding natural disturbance regimes

of forests would allow for a more accurate identification of "true" or "functional" old-growth habitats.

Maintenance of diversity—structural and functional diversity as well as species diversity—is a major issue of concern for resource managers and appears to be one of the key elements for the evolution of the ecosystem management paradigm. Disturbance is believed to play a key role in the expression of biological diversity in natural ecosystems. Disturbance may enhance plant diversity by preventing dominance by a few species (i.e. non-equilibrium coexistence) and/or by creating a heterogeneous landscape that can be utilized by plant species with different niche requirements (Grubb 1977, Pickett 1980, Petraitis et al. 1989). Natural disturbance enhances animal diversity by maintaining structural complexity (Hansen et al. 1991). For example, forest structure determines habitat features such as food abundance, cover, and microclimate (Cody 1985); dead and dying trees are important sources of shelter and food for wildlife (e.g. Nicholls 1994). Because of the link between disturbance and diversity, knowledge of natural disturbance dynamics is important where maintaining biological diversity is a forest management objective (Denslow and Spies 1990).

Knowledge of natural disturbance regimes will also be useful, if not necessary, for restoration of altered, damaged, or destroyed ecosystems. To date, protecting existing diversity and amenity values has been the focus of many resource management activities dealing with nonmarket goods and services; these activities likely will not be adequate in the long-term. Jordan (1988) listed the following reasons for ecosystem restoration:

1) Vast areas have already been profoundly altered by human activity;

2) Human-caused alterations of natural ecosystems will continue to change;

3) Some changes (e.g. global climate change) are beyond human control, but they will change those areas already preserved;

4) Existing wilderness preserves are usually too small or suboptimally shaped or designed; these preserves would be more valuable as biological diversity reservoirs if ecosystems surrounding these preserves were restored, thereby increasing the size of the areas;

5) Habitat restoration is the only hope of long-term survival of some species endangered because of habitat loss; and

6) Conserving species *ex situ* will not be environmentally valuable if habitat can not be provided for them; it may be necessary to create habitat on disturbed sites.

Cairns (1988) suggested that restoring partially or badly damaged ecosystems is probably the best way to increase diversity.

Understanding natural disturbance regimes has implications for ecosystem restoration efforts . "A scientifically defensible approach to restoration requires not only that we know how the existing and "original" forests [or ecosystem of interest] differ, but also that we understand the mosaic of stands [or comparable community unit] on the landscape from a dynamic rather than a static perspective." (Lorimer and Frelich 1994). Natural disturbance regimes can be used as the blueprints necessary to restore ecosystems that function more naturally. Ecosystem management may also involve restoration of ecosystems or communities, both managed and protected, to more "natural" (e.g. presettlement) conditions (e.g. Stritch 1990).

Importance for Modeling

Simulation models are increasingly utilized by natural resource research and management professionals. Models are tools that assist natural resource professionals perform the following functions (Hall and Day 1977):

1) Conceptualizing, organizing, and communicating phenomena;

2) Understanding a system by:

a) Finding emergent properties;

b) Generating hypotheses;

c) Testing validity of field measurements and assumptions; and

d) Making predictions about future or hypothetical states;

3) Assessing environmental impact or change; and

4) Optimizing decision making.

Knowledge of natural disturbance regimes has been incorporated into models, or models have been utilized to understand natural disturbance, in boreal forests (e.g. Kellomäki et al. 1989, Prentice and Leemans 1990, Kellomäki and Väisänen 1991, Hunter 1993), mesic forests (e.g. Bormann and Likens 1979, Shugart 1987, Frelich and Lorimer 1991), subtropical forests (e.g. Shugart 1987), and tropical forests (e.g. Pederson et al. 1991). Models will be utilized even more in the future to better understand and manage for ecosystem and landscape complexity.

SIGNIFICANCE OF THIS RESEARCH PROJECT

Natural disturbance regimes in temperate rainforests of southeast Alaska are poorly understood. Wind is the primary disturbance agent (Alaback 1990, 1991), although forest structure and dynamics are influenced by other disturbance agents such as

landslides, debris flows, soil slumping, insects, fungi, and snow breakage. Spatial scales of these disturbances and forest responses to them vary along the entire spectrum from negligible to landscape-level.

Most of the land area of southeast Alaska is part of the Tongass National Forest and is managed by the USDA Forest Service. The Forest Service has initiated an ecosystem approach to forest management that intends to utilize current ecological knowledge of forest structure and function to modify traditional forest management practices. Ecosystem management is an effort by the Forest Service to address evolving public concerns by practicing sustainable, long-term, multiple use management on commodity production timberlands.

My research focused primarily on small-scale natural disturbance regimes and their variability, and on forest response to small-scale disturbances in the Chatham Area of the Tongass National Forest. Most of my work was conducted in the western hemlock (*Tsuga heterophylla*)/blueberry (*Vaccinium spp.*)/shield fern (*Dryopteris austriaca*) plant association described by Martin et al. (1995). Plant associations in the western hemlock series are very common across the landscape and are of high value for timber production, wildlife habitat, and esthetics. These forest uses typically represent conflicting human demands. The Forest Service is mandated by the National Forest Management Act of 1976 to manage for biological diversity on national forest lands. Understanding forest dynamics in these plant associations, therefore, may be more critical than in plant associations with fewer conflicting human demands (e.g. mountain hemlock [*Tsuga mertensiana*] associations) or in areas that have legal protection (e.g. riparian zones). Increased understanding of forest dynamics will assist forest managers by increasing their ability to manage the forest for human demands

while retaining natural forest processes that maintain long-term forest productivity, structural and functional stability, and biological diversity.

OBJECTIVES OF THIS RESEARCH

My research focused on 3 issues relating to natural disturbance in southeast Alaskan forests. My primary focus was on: (1) characterizing some features of small-scale natural disturbance regimes and their variability in old-growth forests, and (2) determining the effects of small-scale disturbances on the understory light environment and forest structure and composition in the same old-growth forests. The third topic of my research was identification of methods that enabled me to interpret wind and treefall patterns at the site- and landscape-levels in forests of southeast Alaska.

In Chapter 2, I first describe canopy gap dynamics at 3 sites in terms of the proportion of land area in gaps, gap area distributions, frequencies of gapmakers/gap, minimum disturbances/gap, proportions of gapmaker types, and frequency distributions of gapmakers by decay class. Secondly, I characterize the diffuse light environment within the forest understory; discuss gap-phase dynamics of the tree component of the understory; and investigate the relationships of plant species richness, cover, and height to gap size and light intensity.

Chapter 3 discusses the importance, techniques and application of interpreting wind and treefall patterns at the site- and landscape-levels in the complex topography of southeast Alaska. I demonstrate the feasibility of mapping wind flows across a complex terrain using flagged trees, treefall directions of large-scale natural blowdowns, and treefall directions of blowdowns adjacent to clearcuts. I also

demonstrate the usefulness of circular data analysis as a technique to investigate site-level influences of topography, locally destructive winds, and their interaction on individual treefall directions.

Chapter 4 is a synthesis of my research project. I briefly summarize my research results, discuss the ecological significance of those results, and consider the management implications of my research.

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CHAPTER 2

DYNAMICS OF CANOPY GAPS AND THEIR INFLUENCE ON LIGHT ATTENUATION, SPECIES RICHNESS AND COMPOSITION, AND TREE REGENERATION IN THE FORESTS OF SOUTHEAST ALASKA

Abstract. Understanding specific effects of natural disturbance on a forest ecosystem requires knowledge of the disturbance regime and knowledge of the response of the forest to the disturbance regime. In this paper, I describe forest canopy gaps and their influence on (1) the understory diffuse light environment, (2) plant species richness and composition, (3) woody vegetation height, and (4) tree regeneration in 3 forests belonging to the western hemlock/blueberry/shield fern plant association in northern southeast Alaska.

Twenty gaps were sampled at each site using random, line intercepts. Canopy gaps (all ages) comprised about 9% of the forest area; expanded gaps comprised about 27% of the forest area at the 3 sites. Gap and gapmaker characteristics generally were similar among sites. The majority of canopy gaps were < 50 m^2 in area, had a D/H ratio < 0.50, were created from the death of 1 or 2 gapmakers, and had experienced gap expansion. The majority of expanded gaps were < 200 m^2. Gapmakers were usually snapped and relatively young.

Characteristics of the diffuse light environment and its relationship to gap area were similar in the 3 forests. Light levels were greatest and most variable at both the shrub and herb layers in canopy gaps. Both point sample and gap-level light values generally decreased, and were less variable along the gradient from canopy gap to transition gap to closed canopy forest. Interception by shrub layer plants decreased herb layer light levels. The reduction in point sample light levels from the shrub to the herb layer was largest in canopy gaps and least under closed canopy forest, indicating the leaf area index of shrubs was greatest in canopy gaps. The same trend existed at gap-level light intensities for canopy and transition gaps. At a given site, average herb layer light levels were similar across the gradient from canopy gaps to closed canopy forest for point samples. Point sample shrub layer light levels were positively associated with mean and median canopy gap areas for the sites. However, the same association of light intensity and canopy gap area did not exist for herb layer light levels. Herb layer light values are probably influenced more by the nature of light interception by shrub cover than by canopy gap size.

When treated as discrete, static entities, canopy gaps appear to have subtle influences on non-tree plant species richness and composition. Most species did not appear to be specialized to particular light environments within the range of observed diffuse light levels. Understory plant species in the 3 forests appear to be robust in terms of their light requirements compared to the range of light conditions present in

the understory. However, some exceptions did occur. Several common species appear to favor gap environments, and species found in very low abundance that were only present in gaps are species that require higher light environments compared to the more common species. Sorenson Index values indicate that gaps and closed canopy forest generally are very similar in species composition. Of the 3 forest positions, however, canopy gaps and closed canopy forest are the least similar.

No significant relationships were found between shrub layer light levels and the height of the tallest individual of each woody species rooted in the 1 m^2 understory vegetation plots. Mean and median heights of several shrub species were associated with forest position, but the trends were not consistent across all sites.

Canopy gaps appear to influence understory tree dynamics. Established western hemlock and Sitka spruce seedlings appear to benefit from the presence of canopy gaps by experiencing increased growth. However, Sitka spruce appears to have the potential to maintain itself through gap-phase replacement only at one of the 3 sites studied. This site has the largest mean and median gap areas and highest diffuse shrub light levels of the 3 sites.

More significant influence of gaps on forest dynamics would have been detectable if larger spatial and temporal scales had been considered. By limiting the scope of this project to old-growth forests, more significant effects of canopy gaps were probably masked. Gaps comprise part of the fabric of old-growth forests. It is their creation that allows the development of structural and species diversity in the understory of a forest stand that was previously depauperate of both forms of diversity in the middle stages of forest development.

Emulating the small-scale natural disturbance regime probably would be best achieved if single tree selection and small group selection cuts were administered within a stand. Decision rules to determine how many trees to remove to create an "artificial gap" can be derived from canopy gap area distributions, distributions of D/H ratios, and the distribution of the number of gapmakers per gap. A decision rule based on the number of gapmakers per gap would be the easiest to administer on the ground.

INTRODUCTION

The greatest expanse of temperate rainforest is distributed along the northwest coast of North America from Alaska south to Oregon (Alaback 1988). The temperate rainforests of North America are unique because they are dominated by evergreen conifers, unlike deciduous hardwood and mixed hardwood-conifer forests that are typical of all other northern temperate regions. These dominant conifers are

also some of the most massive and longest-lived tree species (Waring and Franklin 1979). The area of southeastern Alaska and British Columbia is one of the rare places where extensive tracts of virgin, northern temperate rainforest still exist (Alaback 1988).

Most of southeast Alaska is part of the Tongass National Forest and is managed by the USDA Forest Service. The temperate rainforests of southeast Alaska are characterized as having a high-frequency, low-intensity disturbance regime (Alaback 1990). These forests are highly susceptible to wind damage due to the combination of shallow root systems, poorly drained soils, and high winds—usually during peak rain intensity (Alaback 1990). Wind disturbance events typically are small-scaled and involve single trees or small groups of trees (Harris 1989, Alaback 1990). Although wind is the primary disturbance agent (Veblen and Alaback 1996), forest structure and dynamics are influenced by other disturbance agents such as landslides, debris flows, soil slumping, insects, fungi, and snow breakage. Spatial scales of these disturbances, and forest responses to these disturbances, vary along the entire spectrum from negligible to landscape-level. The abundant year-round moisture and rarity of lightning storms result in minimal disturbance by fire (Harris 1989, Alaback 1990).

The purpose of this study was twofold. First, natural disturbance regimes in forests of southeast Alaska are poorly understood. Therefore, I characterized the most common form of natural disturbance in southeast Alaskan forests—canopy gap formation. I described canopy gap dynamics of 3 productive forests in terms of the proportion of land area in gaps, gap area distributions, frequencies of

gapmakers/gap, minimum disturbances/gap, proportions of gapmaker types, and frequency distributions of gapmakers by decay class.

Second, only a few studies (e.g. Alaback 1990, Alaback and Tappeiner 1991) have documented understory response to small-scale wind disturbance in southeast Alaska. Generally, forest structure is thought to affect understory vegetation by altering microclimate. In the maritime climate of southeast Alaska, light is believed to be the key environmental factor influencing understory growth (Alaback 1982). Plant species diversity in the region is also related to solar radiation. The greatest species diversity is found on the lowest productivity sites, primarily because more sunlight reaches the understory strata. Conversely, the most productive forests are the least diverse (Alaback 1996). I was interested to see if a light gradient existed from canopy gaps into closed canopy forest, and if solar radiation levels influenced understory vegetation richness and growth on the same scale. I described the influence of canopy gaps on the understory light environment, on plant species cover and richness, and on tree regeneration.

Knowledge of canopy gap dynamics and the influence of canopy gaps on forest structure and function in southeast Alaska will assist forest managers in their efforts to modify current forest management practices to more closely emulate natural disturbance patterns and processes on the Tongass National Forest.

STUDY AREA

Geography and Climate

Southeast Alaska, also known as the Alexander Archipelago, is a region of complex topographic features—steep mountains, glaciers, fjords, straits, channels,

wetlands, and coniferous forests. This region extends north to south 800 km and is about 160 km east to west. The majority of southeast Alaska lies within the boundaries of the Tongass National Forest.

Southeast Alaska has a cool, wet, maritime climate. Annual precipitation ranges between 150 and 500 cm (Harris et al. 1974), with at least 10% occurring during the summer months (Alaback 1991). Precipitation totals are generally heaviest on the outer coast and decline to the east until the eastern side of the innermost islands and the mainland are reached, where total precipitation increases again (Andersen 1955). Mean winter temperatures—December through February—generally decrease in a northwest direction, while mean growing season temperatures—May through September—generally decrease in a northerly direction (Andersen 1955). The July isotherm is $< 16^{o}$ C (Alaback 1991). Wind patterns, ice fields, and other factors influence local rainfall and temperature patterns (Alaback 1982).

Vegetation

Approximately 57% of the land in southeast Alaska is forested, with the remaining area consisting of fresh water, non-forest land (e.g. alpine and wetland), and land developed for purposes other than timber production (USDA Forest Service 1990). Well-developed, closed-canopy forests are found from sea level to about 600 m in elevation. The hemlock-spruce forest type comprises the majority of closed-canopy forests in the region (Alaback 1982). At least seven forest series achieve a late successional sere, and 3 of these are highly productive Sitka spruce (*Picea sitchensis*)-western hemlock (*Tsuga heterophylla)* associations: beach, riparian, and upland (Samson et al. 1989).

Study Sites

Three study sites were located across the northern portion (Chatham Area) of the Tongass National Forest in southeast Alaska (Figure 1). Study sites were classified as belonging to the western hemlock/blueberry (*Vaccinium spp.*)/shield fern (*Dryopteris austriaca*) forest plant association described by Martin et al. (1995). The sites had structural features of old-growth forests such as snags [dead, standing trees]; downed logs; and large, live trees. Site selection was limited to forests in the western hemlock/blueberry/shield fern plant association because these areas are productive well-drained uplands valuable for timber production, wildlife habitat, and esthetics.

Lemon Creek study site.—The Lemon Creek study site is in the Lemon Creek drainage 10 km northwest of Juneau on the mainland (Figure 1). The site is approximately 11 ha in size. The aspect of the site is southeast to southwest and slope values range between zero and 34°. The soil is a well-drained gravelly silt loam of glacial till and colluvial origin; it is classified as a loamy-skeletal, mixed Typic Humicryod (M. McClellan, USDA Forest Service, pers. commun.).

Trees at the Lemon Creek site are comprised almost entirely of western hemlock (Figure 2). The oldest trees are probably 300 to 500 years old. The majority of the dominant and codominant trees have internal decay so their age distribution could not be determined. The diameter distribution of trees suggests that the forest is uneven-aged.

Outer Point study site.—The Outer Point study site is located at the northwest tip of Douglas Island (Figure 1). It is approximately 8 ha in size and is bisected by a

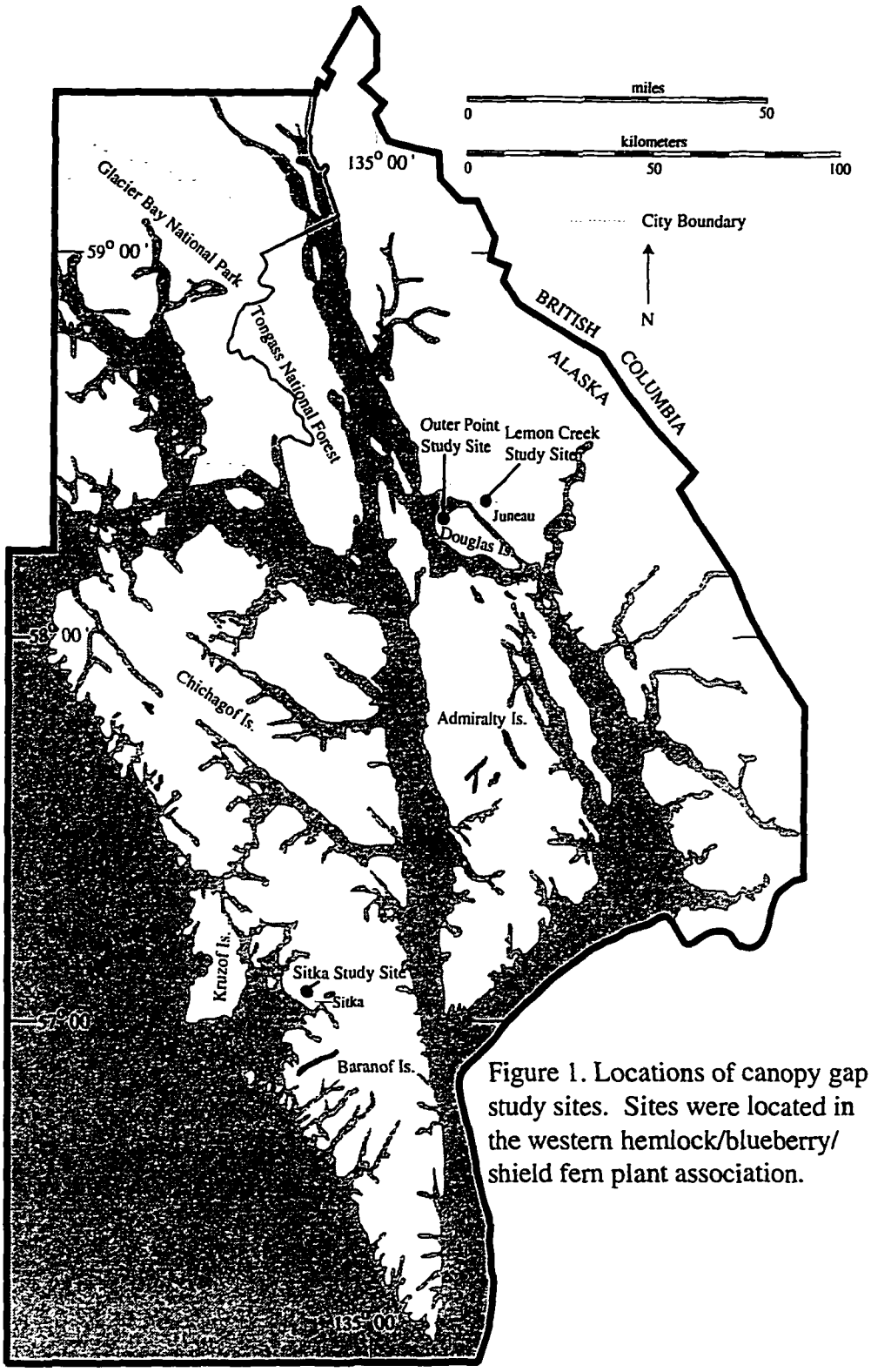

Figure 1. Locations of canopy gap study sites. Sites were located in the western hemlock/blueberry/ shield fern plant association.

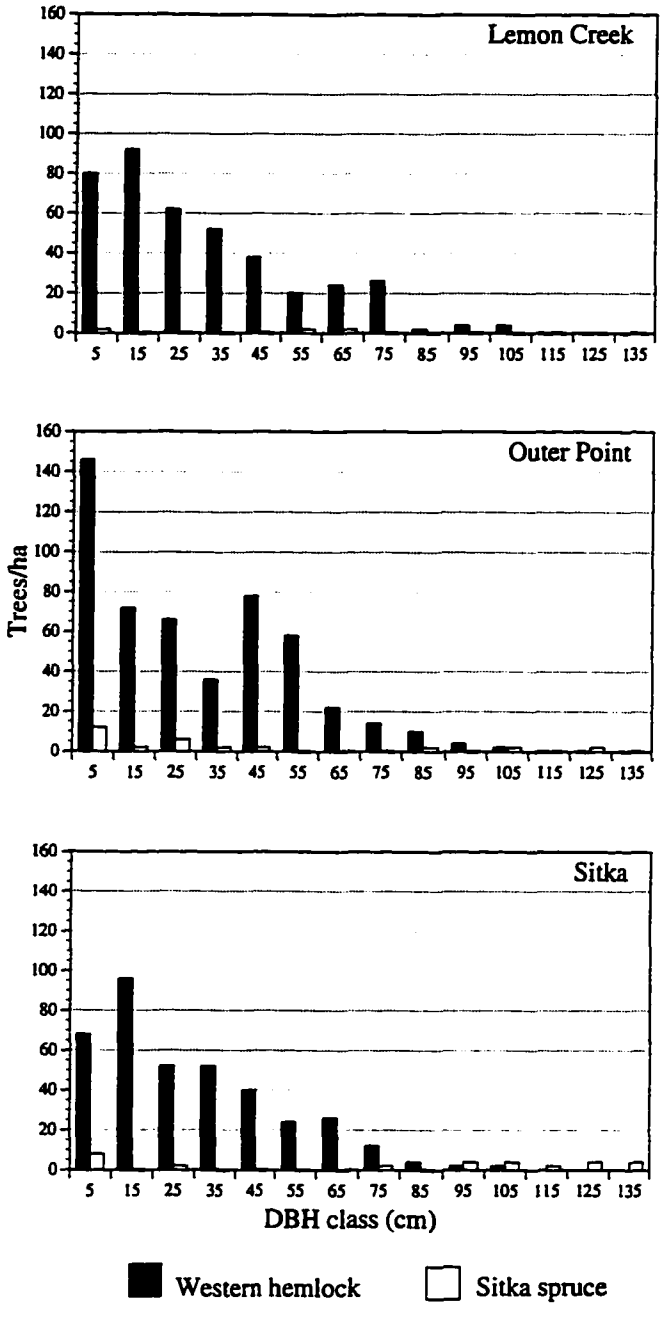

Figure 2. Frequency distributions of tree densities for gap study sites. Tree densities are averages for five 0.1 ha reference plots at each site. The smallest size-class is 2.5-9.9 cm DBH; all other size-classes are 10 cm classes.

drainage that supports a western hemlock/blueberry/skunk cabbage (*Lysichiton americanum*) plant association defined by Martin et al. (1995). The area is fairly level with the slope ranging from zero to 7°.

The soil is moderately well-drained and has several origins. The soil on the east end of the site is derived from both a shale-like bedrock that is weathering in place as well as from colluvium. Soil texture is a silty clay loam; this soil is classified as a loamy-skeletal, mixed Typic Humicryod (M. McClellan, USDA Forest Service and C. Ping, Univ. Alaska Fairbanks, pers. commun.). The soil on the west end of the site is glacial in origin and has a mixed minerology. It is also a loamy-skeletal, mixed Typic Humicryod (M. McClellan, USDA Forest Service and C. Ping, Univ. Alaska Fairbanks, pers. commun.). The soil on the northern section of the site is derived from alluvium over bedrock; it is a relatively young soil. Soil texture of this northern portion of the Outer Point study site is a gravelly sandy clay loam; this soil is classified as a loamy, mixed or loamy-skeletal, mixed Dystric Cryochrept (M. McClellan, USDA Forest Service and C. Ping, Univ. Alaska Fairbanks, pers. commun.).

Western hemlock dominates the Outer Point study site in all but the largest diameter classes, where Sitka spruce dominates. Tree diameter distribution is bimodal (Figure 2). The age distribution of dominant and codominant trees also is bimodal, with the largest peak—22% of a 36 tree sample—in the 225 to 249 year age class, and a smaller peak—about 14% of the sample—occurring between 125 and 149 years (Figure 3). Ages of the dominant and codominant trees ranged from 106 to 331 years.

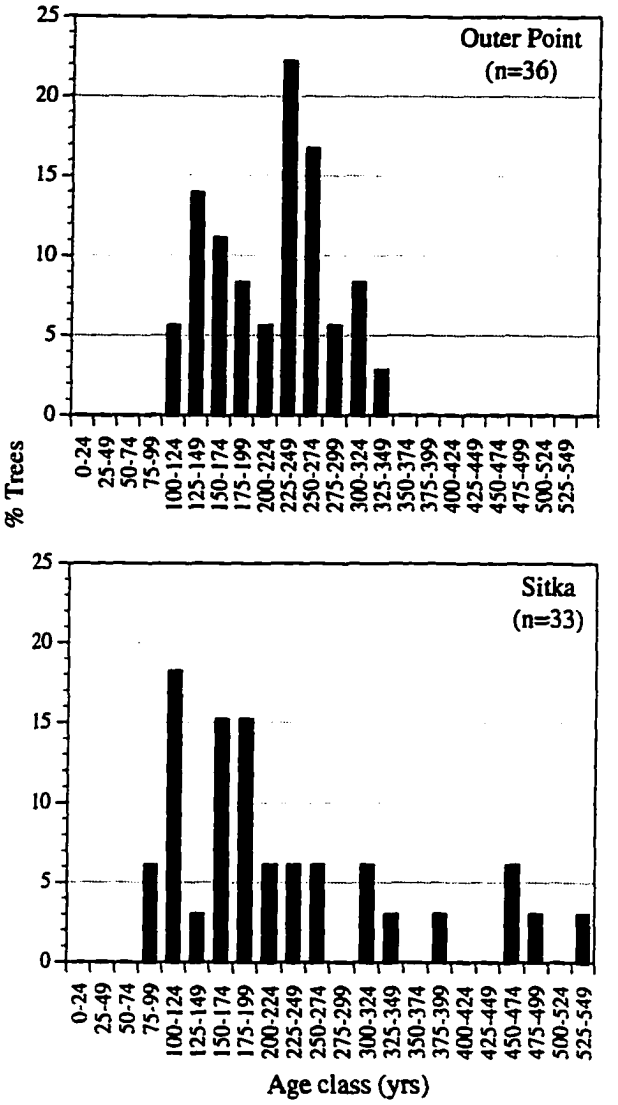

Figure 3. Frequency distributions of minimum tree ages for gap study sites. Ages are for dominant and codominant trees. Trees were cored as close to the root collar as possible, but no correction for tree growth to core height was used. Tree ages for Lemon Creek are not shown because internal decay prohibited aging most trees at that site.

Sitka study site.—The Sitka study site is located on the lower slope of Harbor Mountain east of Sitka and within the city limits (Figure 1). The Sitka site is approximately 7 ha in size. The aspect of this site is west to southwest; slope values range between zero and 45°.

Soil parent material consists of a deep volcanic ash from nearby Mount Edgecumbe on Kruzof Island. Mount Edgecumbe last erupted between 10,600 and 11,400 yr. B.P. (Riehle et al. 1992). The soil is a well-drained, is derived from colluvium, and slip planes are present (R. West, USDA Forest Service, pers. commun.). The soil is classified as medial over coarse loamy Typic Humicryod (R. West, USDA Forest Service and C. Ping, Univ. Alaska Fairbanks, pers. commun.). The site is exposed to an open harbor and is subjected to winds blowing directly from the Gulf of Alaska. Evidence of rockslides is abundant, but the dates of these disturbance events are unknown.

Western hemlock dominates the Sitka study site except in the largest diameter classes, which are comprised entirely of Sitka spruce (Figure 2). The diameter distribution of trees is spatially variable. There are patches where tree diameters are fairly uniform, suggesting an even-aged structure. Other patches have variable diameter distributions more suggestive of an uneven-aged structure. Forest patches tend to be oriented perpendicular to slope contours. The presence of these patches with noticeably different diameter distributions is most likely related to the rockslide activity of the site. Spatial distribution of the largest Sitka spruce appears to be associated with the distribution of rockslide lobes. The age distribution of dominant and codominant trees peaks between 100 and 124 years—about 18% of a 33 tree

sample—and between 150 and 199 years—about 30% of the sample (Figure 3). Ages of the dominant and codominant trees range from 95 to 546 years.

Other sites.—I sampled several other sites in the northern portion of southeast Alaska. However, complete data sets were not collected for these areas. I refer to the Lemon Creek, Outer Point, and Sitka study sites as intensive study sites because complete sets of data were collected at those sites.

I collected information about the proportion of forest area comprised of small-scale natural disturbances in a western hemlock-Sitka spruce complex on Douglas Island, and a western hemlock-Alaska yellow cedar (*Chameacyparis nootkatensis*) and western hemlock-Sitka spruce-Alaska yellow cedar complex on northwest Baranof Island. A complex is a forest in which the plant associations are interspersed at scales smaller than the scale of interest. Specific plant associations were not recorded for these sites.

METHODS

Definitions

I recognized 3 types of gaps related to small-scale natural disturbances of forests: canopy gaps, expanded gaps, and transition gaps. I defined a *canopy gap* as the land surface area directly under a canopy opening (Runkle 1982) that was formed from the death or displacement of a tree crown with an area equal to or exceeding the area occupied by an average codominant tree crown in the surrounding forest. The average width of the canopy gap along its long axis could not exceed the average total tree height of the surrounding forest (i.e. the ratio of average gap width along its long axis to average tree height of the surrounding forest is < 1). The average height of

regenerating trees in the canopy gap could not exceed 50% of the average height of the surrounding forest canopy (i.e. the ratio of the average height of regeneration to average forest canopy height is < 0.5). This definition set minimum and maximum canopy gap areas and identified when the canopy of the tree regeneration in a gap merges with the surrounding forest canopy, thereby closing the gap.

Based on this definition, any canopy opening less than the size of an average tree crown was considered interstitial spacing and no canopy gap existed under it. I felt that defining the minimum canopy gap area as being equivalent to the area of one tree crown would enable forest managers to more easily apply results of this research; emulating natural disturbance patterns would entail removing one or more tree crowns.

It has been suggested that maximum gap size be ≤ 10 canopy trees (Christensen and Franklin 1987) or have a canopy height-gap diameter ratio equal to 1 (Runkle 1992). I felt the latter approach was more appropriate because it is based upon a functional role of gaps in forests (see the discussion on gap D/H ratios). However, defining maximum gap size using a simple canopy height-gap diameter ratio does not recognize the importance of gap shape. A long, narrow gap may have a canopy height-gap diameter ratio > 1, but still function as a canopy gap. For this reason, I chose to use a modification of the canopy height-gap diameter ratio that takes gap shape into account. A canopy gap where the *average width along its long axis* exceeded the average total height of the surrounding forest was considered too large for the purposes of this study. The simultaneous death of more than a few trees is more appropriate for studies of stand-replacement disturbances or studies of succession after large-scale disturbances (Runkle 1992). In hardwood forests in

southern Illinois, for example, Minckler and Woerheide (1965) determined that creating openings whose diameters exceeded the height of the surrounding forest canopy had little additional effect on plant species composition or growth of reproduction.

The definition of a canopy gap must distinguish when a gap merges with the surrounding forest canopy. Canopy gap closure occurs by way of 2 processes: (1) lateral expansion of canopy tree crowns, and (2) height growth of tree regeneration in a gap. Based upon my definition, a canopy gap merges with the forest canopy when lateral expansion reduces gap area to less than the area of an average tree crown, or when regeneration in a gap is > 50% of the height of the surrounding forest canopy.

Expanded gaps were relatively simple to identify compared to canopy gaps. Runkle (1982) defined an *expanded gap* as consisting "of the canopy gap plus the adjacent area extending to the bases of canopy trees surrounding the canopy gap." I utilized the same definition. The concept of the expanded gap is important because expanded gaps include areas directly and indirectly influenced by the canopy opening (effects of light are often offset from the gap center). Measuring only canopy gaps underestimates the importance of gaps in a forest community (Runkle 1982).

A *transition gap* consisted of the area of the expanded gap that is under forest canopy. In other words, it represents the difference in area between the expanded gap and the canopy gap.

A *gapmaker* is a tree whose death—or crown displacement in the case of leaning trees—results in the creation or expansion of a canopy gap. I recognized four gapmaker types: dead standing, snapped, root-thrown, and leaning.

A *perimeter tree* is a tree whose crown helps form the boundary of a canopy opening.

A *gap tree* is a tree rooted within an expanded gap that has a DBH ≥ 2.5 cm and whose height is less than half the average height of the canopy surrounding the gap.

A *replacement tree* is a tree that is likely to replace a gapmaker or fill all or part of a canopy opening. A replacement tree is also a gap tree.

Log decay classes were used as a relative ranking indicating the degree to which a gapmaker was decomposed; class 1 logs were the least decayed and class 4 + logs were the most decayed. The decay classes emphasized the presence or absence of fine branches (< 2.5 cm) and the degree of structural support of a log:

Class 1: Solid, self-supporting log with fine branches and without sloughing bark;

Class 2: Solid, self-supporting log without fine branches;

Class 3: Log that is sagging but still has some support points;

Class 4: Identifiable log that follows the contour of the ground;

Class 4+: A log that is decayed to the point where it is becoming incorporated into the forest floor or a stump that does not have an accompanying log.

I developed this log decay class rating system because some characteristics of the 5-class systems for Douglas-fir (*Pseudotsuga menziesii*) trees in the Pacific Northwest (e.g. Spies and Cline 1988) are not applicable to trees of southeast Alaska. Also, characteristics of class 5 logs are rarely, if ever, observed in Southeast Alaska because of the presence of a thick moss layer or other organic debris.

I did not use a 1-5 log decay class rating system because I did not want readers to confuse my decay class rating system with the well-established systems used in the

Pacific northwest. However, I felt that a 5 class rating system was warranted. Decay class 4+ gapmakers usually were stumps without an associated log whereas class 4 gapmakers were all identifiable logs.

Characteristics of Gaps and Gapmakers

Data were collected from June through August, 1991-1993. Gaps that were to be sampled were identified using the line intersect sampling design outlined by De Vries (1979). A sample line began at a boundary of a study site, passed through a pre-selected random point along a pre-selected random orientation, and ended when another boundary of the same study site was encountered. Detailed information was collected only in those gaps where the sample line crossed the long axis of the expanded gap. The probability of encountering small gaps was the same as the probability of encountering large gaps because line intersect sampling is not size biased (P. Quang, Univ. Alaska Fairbanks, pers. commun.). Also, a sampling bias due to a pronounced trend of the long axes of the gaps to be oriented in one direction (De Vries 1979) did not occur in this study. A gap could only be sampled once because line intersect sampling is a form of random sampling without replacement. However, the length of each sample line that passed through canopy gaps and transition gaps was recorded for all gaps that were encountered, not just those that were intensively sampled.

Twenty gaps were sampled at each site. A minimum of 1000 m of sample lines were measured at each site in order to estimate the proportions of land area in gaps or under forest canopy, regardless of the number of gaps that were encountered.

However, more than 1000 m of lines were sampled if they were needed to locate the minimum sample size of 20 gaps.

The total length of all randomly oriented sample lines was measured and subdivided into length within canopy gaps, expanded gaps, and under forest canopy (Runkle 1982). The proportions of land area in gaps and under forest canopy were calculated from the sample line lengths in the three subdivisions.

Gap area was determined using 2 methods. In the first method the lengths of the small and long axes were measured for single treefall gaps, and for multiple treefall gaps that were elliptical in shape. Gap areas were then calculated using the formula for the area of an ellipse (Runkle 1982, Foster and Reiners 1986). In the second method gap perimeters were traversed with a measuring tape and compass to yield a series of vectors (Foster and Reiners 1986). Gap areas were calculated from the vector lengths and directions using AREA, a microcomputer program (Saalfeld 1982). This method was used for multiple treefall gaps with irregular perimeters. Gap size distributions were constructed by grouping gaps into 25 m^2 classes.

Canopy gap sizes were compared to the height of the surrounding forest by calculating the D/H ratio, known as the index of size of a clearing (Geiger 1965). The D/H ratio is a comparison of the idealized canopy gap diameter (D)—where the gap is assumed to be a perfect circle—to the average height of the perimeter trees surrounding a canopy gap (H). This ratio is probably more indicative of the functional role of gaps in forest settings compared to expressing gap areas in absolute terms. A larger D/H ratio indicates a larger gap relative to the height of the surrounding forest. As the D/H ratio increases, it is expected that a greater difference will exist in the microclimate in the gap (e.g. higher light levels) relative to the

surrounding forest. It is to be expected that a threshold D/H ratio exists, above which the microclimate becomes extreme relative to the forested environment (Geiger 1965). Identification of this threshold D/H ratio for a forest type or geographic location could lead to objective definitions of small-scale and large-scale disturbances.

General descriptors of gapmakers were collected and summarized. Data relevant to this study that were collected for gapmakers included: gapmaker type, species, and decay class. Proportions of gapmaker types were calculated, and distributions of the number of gapmakers per canopy gap and proportions of gapmakers by decay class were determined.

The number of different decay classes of gapmakers represented in each gap was used to determine the frequency distributions of the minimum number of disturbances that occurred in each canopy gap. The maximum number of disturbances per gap that could be identified was 5, equal to the number of log decay classes that were used.

Vegetation Structure and Species Richness

Gap vegetation structure and species richness were described in the 20 gaps sampled at each site. Between 10 and 20 1-m^2 understory vegetation plots were sampled in each expanded gap. The number varied depending on gap size and shape. Understory vegetation plots were placed systematically along the long axis of each gap, and along one or two perpendicular short axes, depending upon gap size.

DBH and species were recorded for all gap trees; characteristics of gap trees were summarized. Up to 3 replacement trees were identified in each expanded gap and

their heights were measured. The criteria used to select replacement trees was height, vigor, position in the gap, and stability of the root system.

The frequency of Sitka spruce replacement trees was compared to the frequency of Sitka spruce gapmakers and live overstory trees to determine if spruce regeneration in small-scale disturbances has the potential to maintain the current proportion of spruce in the stands. I assumed that spruce has the potential to maintain its current position in a stand if its proportion as replacement trees is ≥ the proportion of spruce gapmakers and live, overstory trees.

Spearman rank correlation coefficients were calculated to determine if associations existed between the number of gap trees per expanded gap and expanded gap area, and between expanded gap tree density and expanded gap area. The Spearman rank correlation was used because gap area distributions were not normally distributed.

Canopy cover (%) of shrubs, trees < 2.5 cm DBH, herbs, and 4 common mosses was measured by species within the 1-m^2 understory vegetation plots within the gaps and reference plots. Vegetation cover classes were as follows:

0-5%—1% cover classes,

>5-10%—10% cover,

>10-100%—10% cover classes.

Vegetation cover was always rounded up when recorded (e.g. plant cover in the range of >10-20% was recorded as 20% cover). The height of the tallest individual of each shrub species rooted within each 1-m^2 plot also was measured.

Spearman rank correlation coefficients were calculated to determine if associations existed among cover values of plant species—and groups of plant

species—and diffuse light levels (described below) and gap areas separately; between plant species richness and diffuse light levels and gap areas separately; and between vegetation heights and diffuse light levels. Cover values of groups of plant species (e.g. fern layer and herb layer) were calculated by adding the cover class values of individual species within a group. These cover values of groups of species are best viewed as an index of plant cover because of the positive bias that exists when adding cover class values that were already rounded up.

Spearman's correlation was used because distributions of gap areas and radiation values usually were not normally distributed. I considered a correlation to be biologically significant if $r \geq 0.50$, and statistically significant if the associated p-value was ≤ 0.10. I referred to a correlation as being significant only when it was both biologically and statistically significant. I chose this conservative approach, because large sample sizes can indicate a statistically significant relationship that may not be biologically meaningful.

Characterization of Light Environments

An instantaneous measurement of photosynthetic photon flux density (PPFD; $\mu E \cdot m^{-2} \cdot s^{-1}$) was recorded over both the shrub and the herb layers at the center of each 1-m^2 understory vegetation plot and midway between all vegetation plots. PPFD was measured using a datalogger equipped with a quantum radiometer (Licor, Inc. LI-190) with a spectral sensitivity of 400-700 nm (PAR) and a 160° angle of acceptance. Instantaneous PPFD measurements were taken only between 1000 and 1500 hrs on totally overcast days. Recording PPFD on overcast days minimized effects of sunfleck activity. PPFD was recorded as soon as the datalogger indicated a

stable reading; the time of each reading was recorded to the nearest minute. Shrub layer PPFD was measured at a height of 1.5 m or at a height equal to the tallest portion of the shrub canopy within a plot, whichever was tallest. Herb layer PPFD was measured at a height equal to the top of the tallest portion of the herb layer canopy (including ferns) within a plot.

PPFD was continuously recorded at one point at a height of 1.5 m in an open area adjacent to each study site during the time instantaneous PPFD readings were being measured within a study site. Open sky PPFD was recorded at 10 sec intervals and averaged for each minute using a datalogger equipped with another LI-190 quantum radiometer.

PPFD values in the forest were expressed as % open sky radiation. Light microclimate was summarized for point sample data for both the shrub and herb layers in 3 forest positions: canopy gaps, transition gaps, and under closed canopy forest. Radiation was also averaged on a per gap basis for the shrub and herb layers in both canopy gaps and transition gaps. Radiation averages were only calculated for canopy and transition gaps with ≥ 5 point samples. Radiation values were not averaged for closed canopy forest because point sample data in this forest position did not represent discrete replicates. Closed canopy forest was only sampled in the 0.5 ha reference plots which were a mosaic of gap and non-gap environments.

Spearman rank correlation coefficients were calculated to determine if associations existed between various combinations of point sample radiation values at the shrub and herb layers and canopy and transition gap areas, and gap-level average shrub and herb light levels and gap areas. Spearman's correlation was used because distributions of gap areas and radiation values usually were not normally

distributed. A correlation was considered to be significant if $r \geq 0.50$ and if the associated p-value was ≤ 0.10 for the reasons described above in the section on vegetation structure and species richness.

RESULTS

Sampling Effort to Locate Gaps

The effort required to locate 20 gaps varied among the study sites. At Lemon Creek, 1982.0 m of lines were sampled in order to locate 20 gaps for intensive sampling. At Outer Point, 2264.5 m of lines were sampled, while only 1001.0 m of lines were required at the Sitka site.

Proportion of Land Area in Gaps

The proportion of forest land area in canopy gaps ranged from 5.8% at Lemon Creek to 12.6% at Sitka; the average amount of land area in canopy gaps was 8.7% (Figure 4). The proportion of forest area in expanded gaps ranged from 18.1 to 43.9% and averaged 27.4% (Figure 4). Estimates of the amount of forest area in canopy gaps from the intensive study sites were comparable to the amount of area in canopy gaps at a site characterized by a western hemlock-Sitka spruce complex on Douglas Island (Table 1). However, a western hemlock-Sitka spruce-yellow cedar complex on northwest Baranof Island had 34% of its area in canopy gaps and a western hemlock-yellow cedar complex had 23% of the forest area in canopy gaps (Table 1).

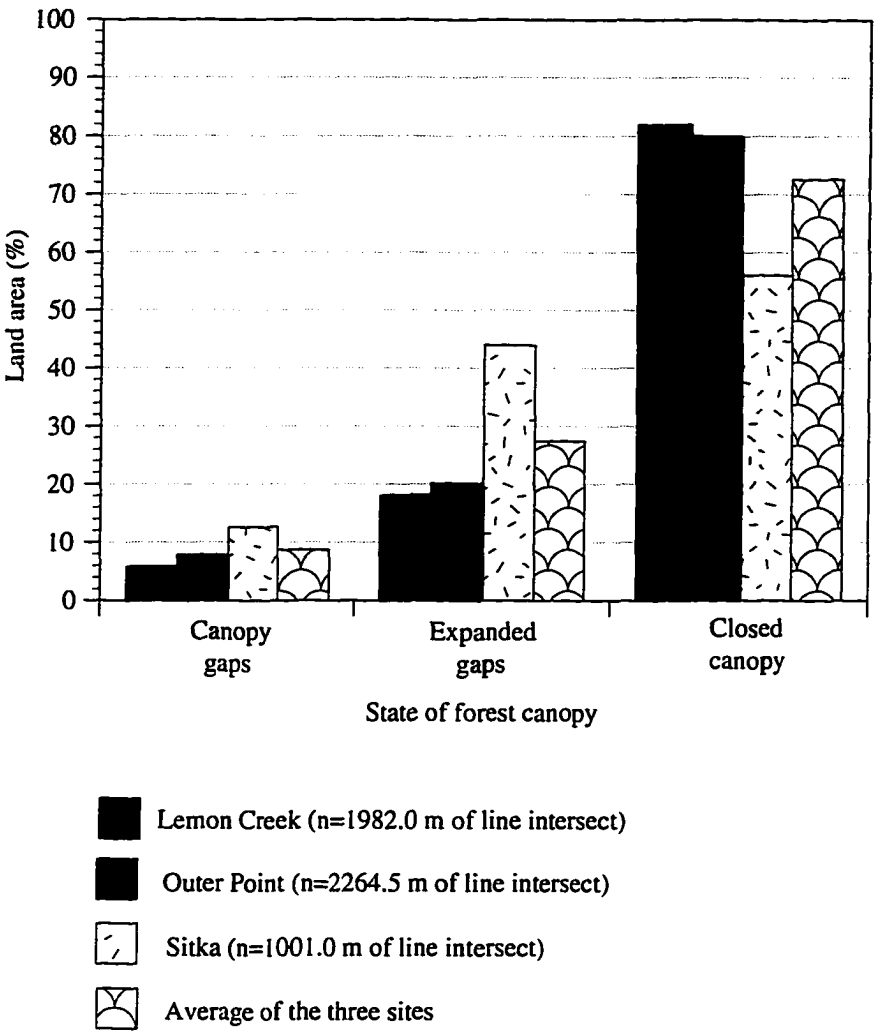

Figure 4. Percentage of land area in gaps and closed canopy forest.

Table 1. Comparison of forest area comprised of canopy gaps (CG) and expanded gaps (EG). Values from selected old-growth and mature forests stands from the literature are compared against values derived from this study. Ranges of forest area in gaps for some studies are given in parentheses.

Forest type [1]	Region	% CG	% EG	Source
Tsuga	Alaska	5.8	18.1	This study (Lemon Creek)
		7.8	20.1	This study (Outer Point)
		12.6	43.9	This study (Sitka)
		8.7	27.4	This study (mean value)
Tsuga-Picea complex [2]	Alaska	7.4	18.2	This study (Douglas Island)
Tsuga-Picea-Chamaecyparis complex [3]	Alaska	33.7		This study (Northwest Baranof Island)
Tsuga-Chamaecyparis	Alaska	23.1		This study (Northwest Baranof Island)
Picea -Tsuga	Oregon	16.3 (14.2-18.4)		Taylor 1990 (2 sites)
Pseudotsuga	Oregon/Washington	18.2	41.7	Spies et al. 1990 (mature)
		13.1	25.5	(old-growth)
Abies-Tsuga-Chamaecyparis	British Columbia	18 (12-22)	71 (69-72)	Lertzman and Krebs 1991 (4 sites)
Picea-Abies	Vermont	> 40 (28-63)		Perkins et al. 1992 (1 site, 5 elevations)
Picea-Abies-Betula	New Hampshire	24		Foster and Reiners 1983
Fagus-Acer-Fraxinus-Quercus	New York	8.4	20.7	Krasny and Whitmore 1992

Table 1 continued

Forest type [1]	Region	% CG	% EG	Source
Acer-Fagus	Ohio	7	14.1	Runkle 1990
		2.7	10.1	Cho and Boerner 1991 (2 sites)
		(2.6-2.8)	(9.1-11.0)	
Quercus-Fraxinus	Indiana	9		Ward and Parker 1989
Tsuga-Betula-Acer-Abies-Thuja	Wisconsin/Michigan	3.1-16.9		Tyrell and Crow 1994 (25 sites)
Mesic (mixed species)	Eastern North America	9.5 (3.2-24.2)	21 (6.7-47.0)	Runkle 1982 (14 sites)
Abies-Acer-Quercus-Tilia	Japan	21.5		Ishikawa and Ito 1989
Fagus-Abies	Japan	18.5		Nakashizuka 1989
Fagus	Japan	18.6		Nakashizuka 1987
Pinus-Quercus	Mexico	18.1		Arriaga 1988
Tropical moist	Panama	3.8		Lang and Knight 1983
Amazonian tierra firme	Venezuela	~ 5		Uhl et al. 1988
Lowland Dipterocarp	Malaya	9.9		Poore 1968
Nothofagus-Weinmannia	New Zealand	37.3		Stewart 1986 [4]
		30.6		
		8.6		
		12.5		

Table 1 continued

Forest type [1]	Region	% CG	% EG	Source
Nothofagus	New Zealand	3.7, 4.1	11.4, 12.9	Stewart et al. 1991 [5]
		14.4, 14.9	25.2, 30.7	
		9.8, 10.7	24.8, 28.8	
Dacrydium-Prumnopitys	New Zealand	2.5	3.8	Ogden et al. 1991
Dacridium-Phyllocladus	New Zealand	2.8	4.5	Ogden et al. 1991
Amomyrtus-Laurelia	Chile	29		Armesto and Fuentes 1988

[1] Forest type was classified by genus names of dominant overstory tree species when possible.

[2] Western hemlock/blueberry, western hemlock/devil's club (*Oplopanax horridum*)-shallow soils, and western hemlock/blueberry-devil's club "patches' were mixed with Sitka spruce/devil's club upland "patches". A plant association complex occurs when plant plant associations are interspersed at scales smaller than the scale of interest.

[3] Well-drained to moderately drained *Tsuga-Picea-Chamaecyparis* "patches" were complexed with poorly-drained *Tsuga-Picea-Chamaecyparis* "patches" and devil's club drainages. Specific plant associations were not recorded

[4] Sites are displayed separately because they had distinctly different disturbance histories.

[5] Two methods of estimating gap area were used.

Gap Characteristics

Differences existed among the specific shapes of the frequency distributions of canopy gap areas of the 3 intensive study sites. However, the frequency distribution of canopy gap areas averaged for the 3 sites exhibited a general exponential decrease in the number of gaps with increasing gap size (Figure 5).

Canopy gaps were skewed toward smaller sizes at all 3 sites (Figure 5). Between 45 and 60% of canopy gaps were < 50 m^2 in size, 60 to 90% of all canopy gaps were < 75 m^2 in size, and 80 to 90% of all canopy gaps were < 100 m^2. On average, the modal canopy gap area—30% of the gaps—was 25 to 49 m^2 in size.

Frequency distributions of expanded gap areas were also skewed toward smaller sizes at all sites (Figure 6). As was the case for canopy gaps, the average frequency distribution of expanded gap areas exhibited a general exponential decrease in the number of gaps as expanded gap area increased. Between 50 and 65% of expanded gaps on a site were < 200 m^2, and 75 to 90% were < 300 m^2. The modal expanded gap area, on average, was 125-149 m^2.

Mean canopy gap area for the intensive study sites ranged from 52 to 70 m^2; mean expanded gap area ranged from 176 to 248 m^2 (Table 2). Areas of both gap types were highly variable, with standard deviations varying between 51 and 100% of mean gap area estimates. Median gap area is a more appropriate statistic than mean gap area because gap areas were not normally distributed (Figures 5 and 6). Median canopy gap areas ranged from 38 to 53 m^2; median expanded gap areas ranged between 158 and 200 m^2 (Table 2).

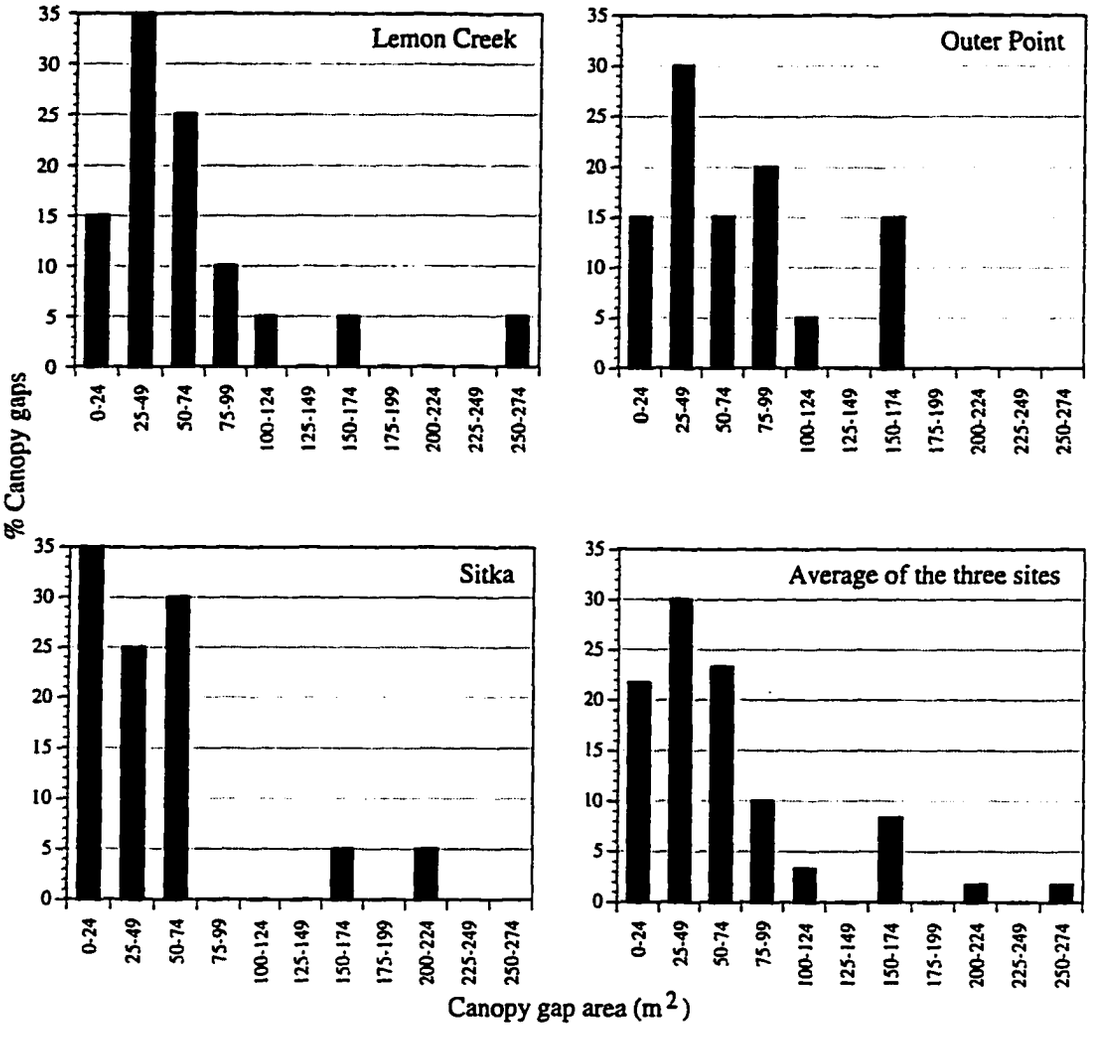

Figure 5. Frequency distributions of canopy gap areas. Twenty gaps were sampled at each site.

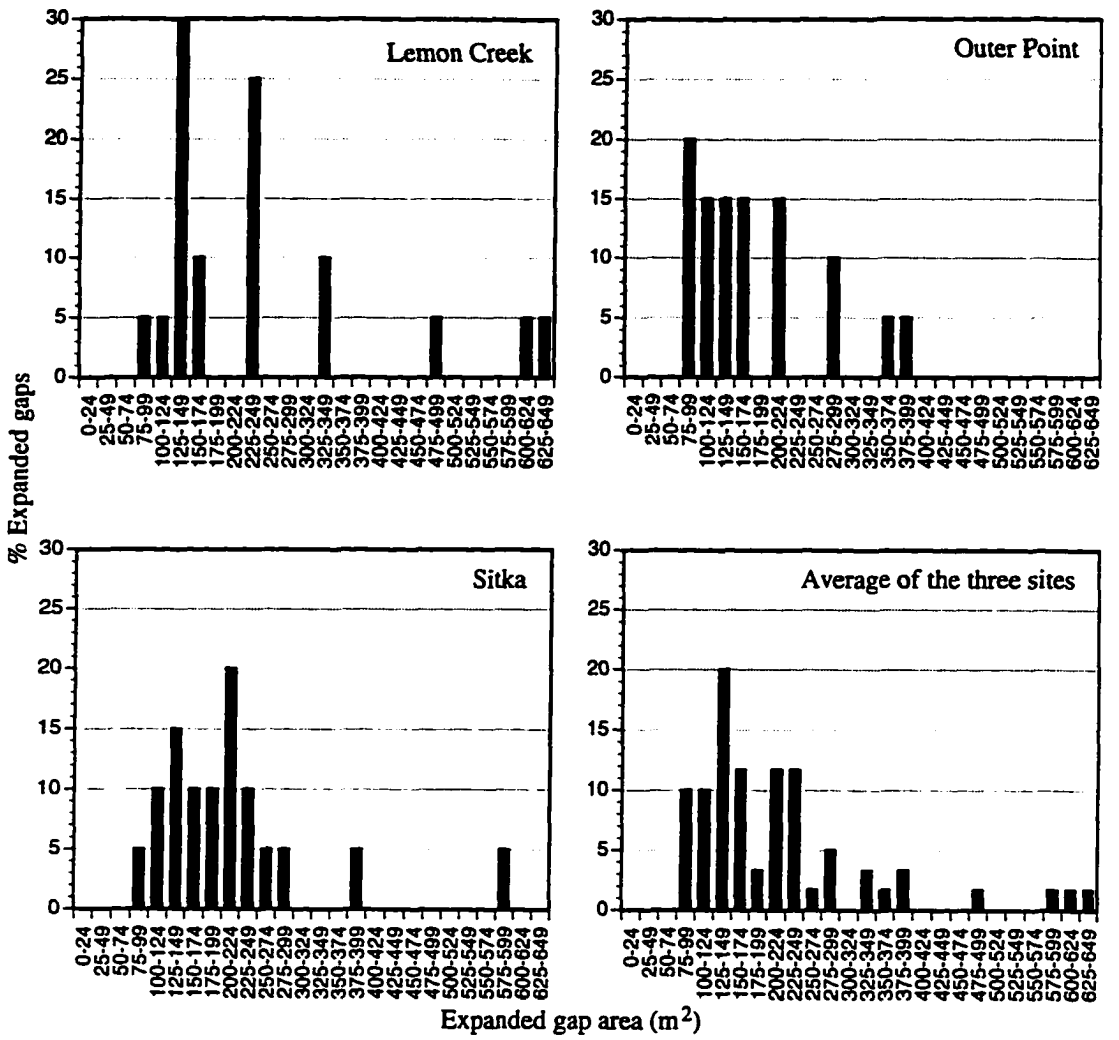

Figure 6. Frequency distributions of expanded gap areas. Twenty gaps were sampled at each site.

Table 2. Canopy gap and expanded gap areas for selected forest types.

Forest type [3]	Region	CG [1] area (m^2)			EG [2] area (m^2)			Source
		Mean	SD [4]	Median	Mean	SD	Median	
Tsuga	Alaska	352	343	208				Hocker 1990
		108	49	100				
		66	60	48	248	160	199	This study (Lemon Creek)
		70	49	53	176	93	158	This study (Outer Point)
		52	52	38	216	110	200	This study (Sitka)
		63	54	46	213	121	186	This study (mean value)
Pseudotsuga	Oregon/			19				Spies et al. 1990 (mature)
	Washington			85				(old-growth)
Abies-Tsuga-Chamaecyparis	British Columbia	77	108	41	286	244	203	Lertzman and Krebs 1991
Picea-Abies	Vermont	96			170			Perkins et al. 1992
Fagus-Acer-Fraxinus-Quercus	New York	42.8			209.1			Krasny and Whitmore 1992
Acer-Fagus	Ohio	25.9	20.3		28.1	59.1		Cho and Boerner 1991
		34.2	58.9		154.4	134.4		
Quercus-Fraxinus	Indiana	52.8	54.3					Ward and Parker 1989
Abies-Betula	China			67			194	Taylor and Zisheng 1988
				55			193	
Fagus-Abies	Japan	65						Nakashizuka 1989

[1] CG = Canopy gap

[2] EG = Expanded gap

[3] Forest type was classified by genus names of dominant overstory tree species when possible.

[4] SD = Standard deviation

Canopy gaps were small relative to the height of the surrounding forest. D/H ratios ranged between 0.08 to 0.62 across all sites, with 95 to 100% of the canopy gaps having ratios < 0.50 (Figure 7). On average, almost 75% of the canopy gaps had idealized diameters that were ≥ 10 and < 30% of the average height of perimeter trees surrounding the gaps. Average perimeter tree heights varied between 31 and 39 m across the sites. Mean D/H ratios were 0.25 at Lemon Creek, 0.29 at Outer Point, 0.20 at Sitka, and 0.24 overall.

Creation of canopy gaps was attributed to the death of a small number of gapmakers per disturbance event (Figure 8). The majority of canopy gaps on all sites—50 to 80%—had only 1 or 2 gapmakers. Between 75 and 90% of all canopy gaps had ≤ 3 gapmakers; no canopy gap had more than 7 gapmakers.

The majority of canopy gaps were multiple treefall gaps. Canopy gaps with multiple gapmakers represented between 65 and 90% of all gaps, and represented 75.1% of all gaps averaged across the sites (Figure 8). Gaps created from 2 gapmakers were the most common type of gap at Lemon Creek and Sitka, as well as overall.

Canopy gaps sampled at a point in time are static entities. In actuality, they are dynamic phenomena that are created, sometimes expand, and usually disappear. Gap expansion events are reflected by the presence of gapmakers in more than 1 decay class within a single canopy gap. On average, the majority (52.6%) of canopy gaps on the 3 intensive study sites have experienced gap expansion (Figure 9). The proportion of canopy gaps that have experienced gap expansion is least at Lemon Creek (40.0%) and greatest at Sitka (65.0%).

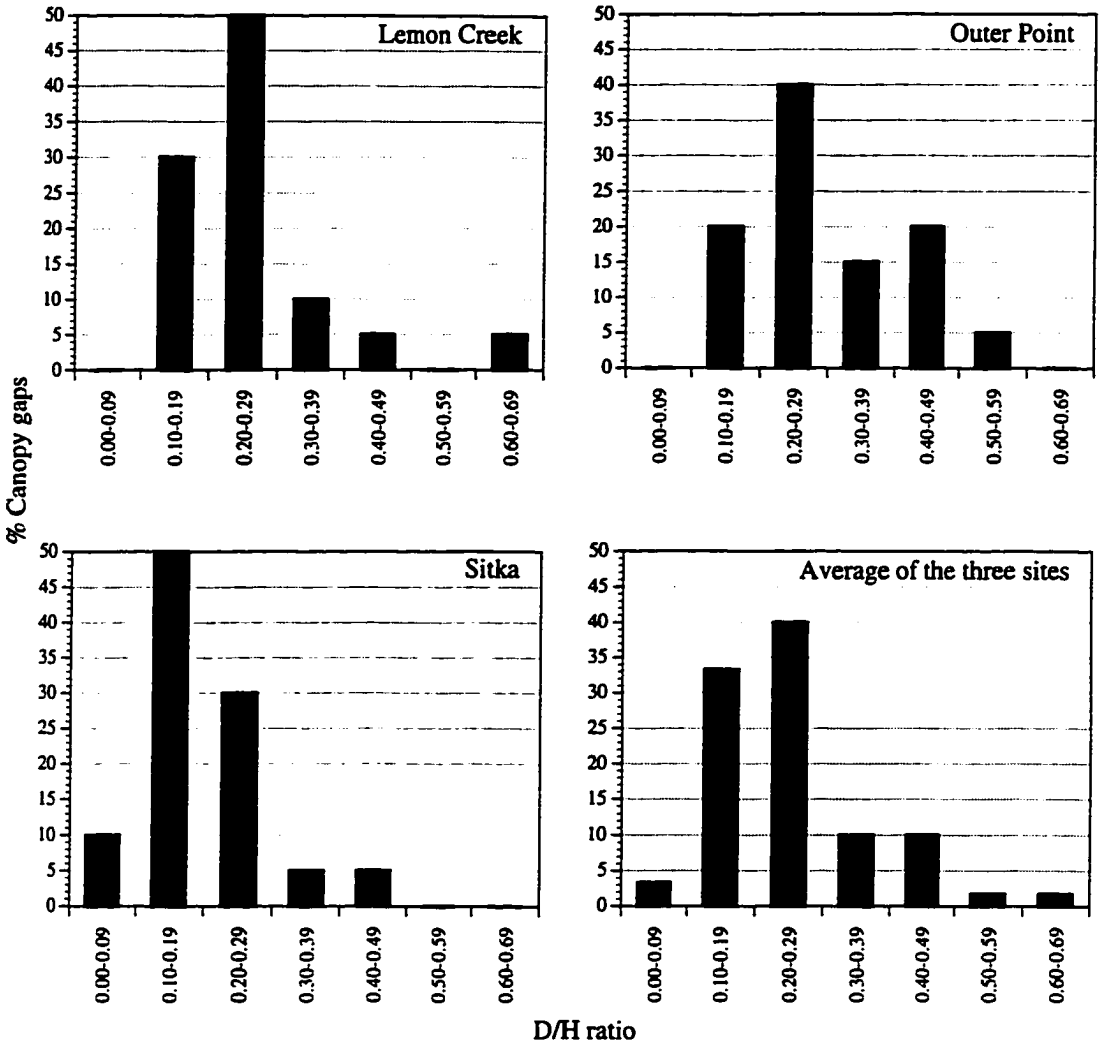

Figure 7. Frequency distributions of canopy gap D/H ratios. Twenty gaps were sampled at each site.

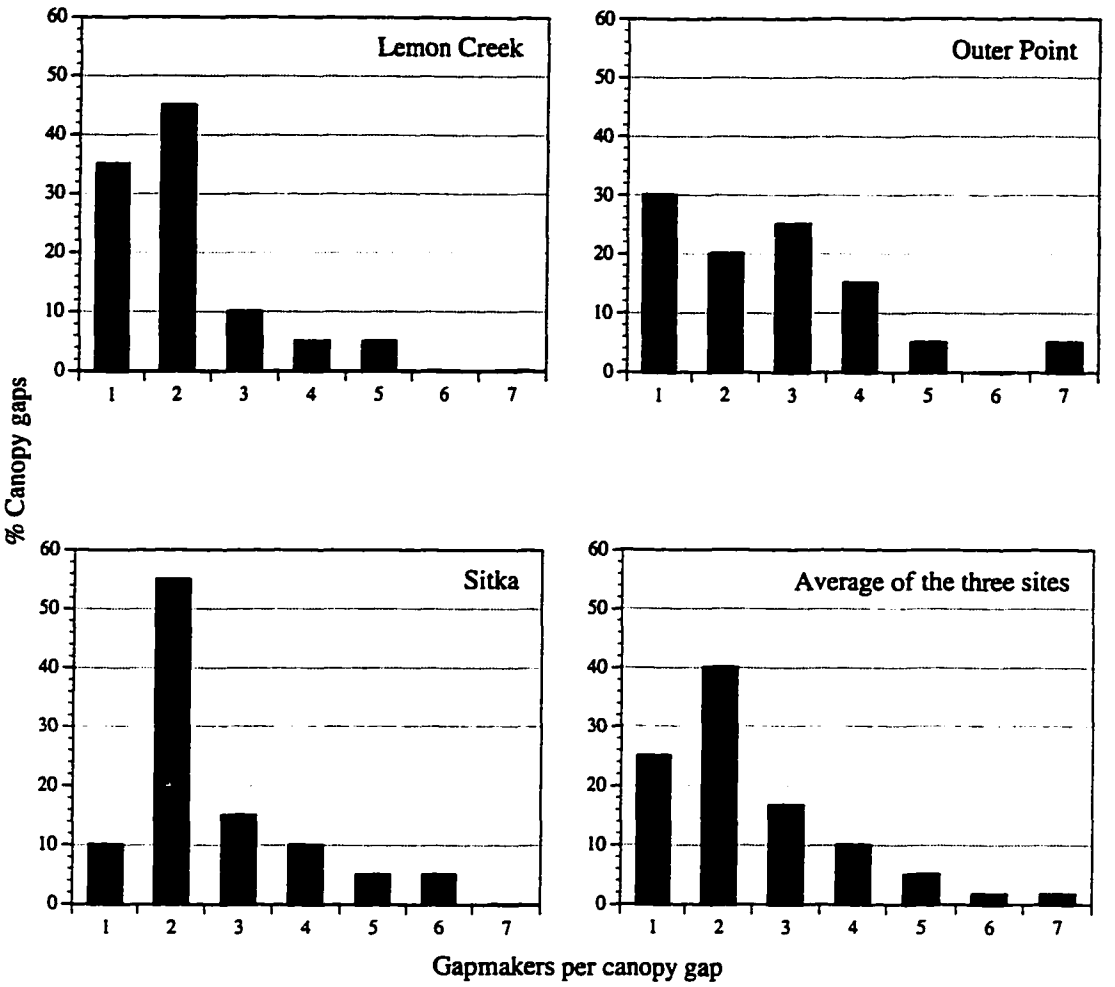

Figure 8. Frequency distributions of gapmakers per canopy gap. Twenty gaps were sampled at each study site.

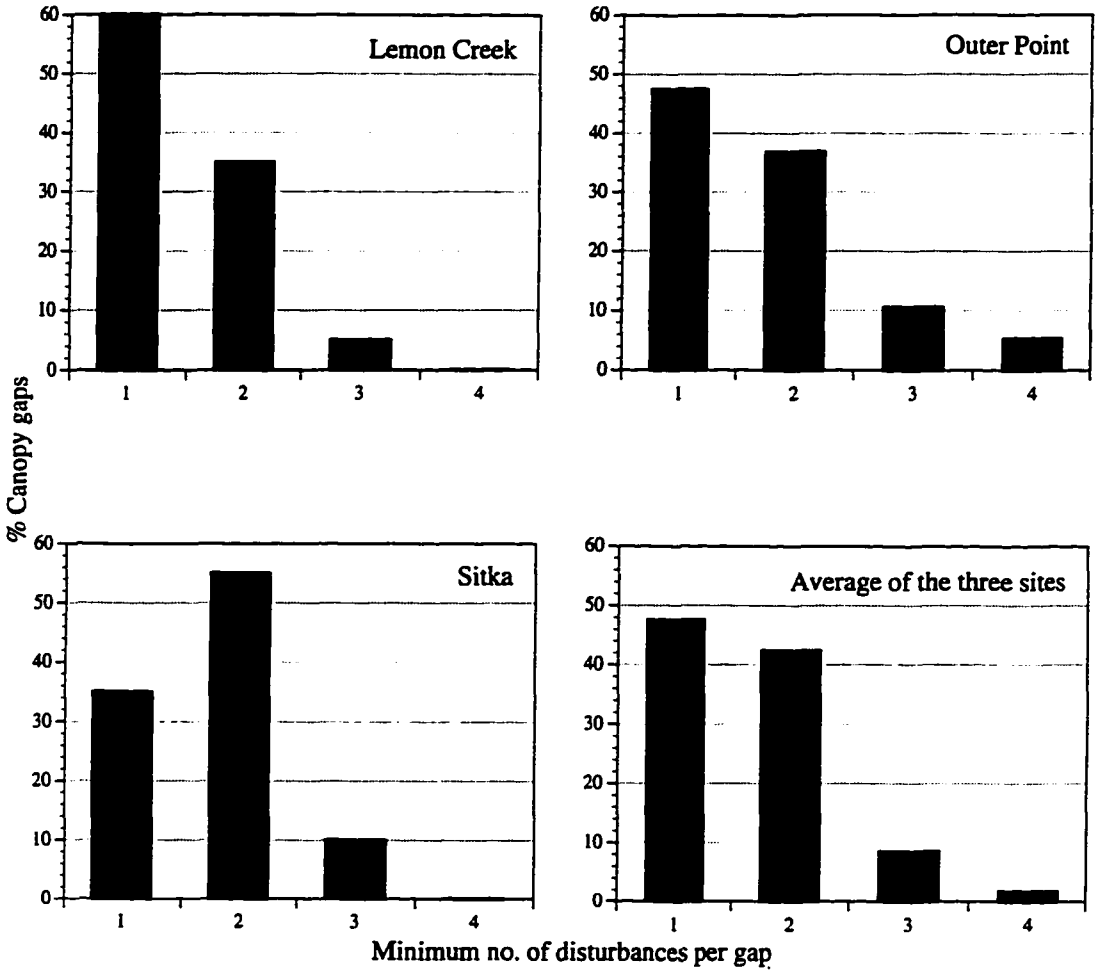

Figure 9. Frequency distributions of the minimum number of disturbances per gap. The number of disturbances per gap was based on gapmaker decay class distribution. Twenty gaps were sampled at Lemon Creek and Sitka; 19 gaps are represented at Outer Point.

Gapmaker Characteristics

The overall order of gapmaker types, from most to least common, was: snapped, root-thrown, dead standing, and leaning (Figure 10, Table 3). Snapped gapmakers predominated at all 3 sites and varied between 64.2 and 95%. Root-thrown gapmakers were the most common at Sitka (25.5%) and dead standing gapmakers were most common at Outer Point (15.1%). Leaning gapmakers were only present in very small proportions (≤ 2.0%) at the Outer Point and Sitka sites. A leaning gapmaker is a partially uprooted live tree in which the live crown has been displaced enough to contribute to the formation of a canopy gap.

Gapmakers were distributed across all decay classes at all 3 intensive study sites (Figure 11). The majority of gapmakers—50 to 64%—were decay class 1 or 2. There was an overall reduction of the number of gapmakers with increasing age from decay class 1 through 4 as inferred from the decay class distribution of gapmakers. Between 14 and 27.5% of gapmakers were decay class 4+.

Light Environment

Light data for all sites are summarized in Tables 4 and 5. However, only the Lemon Creek data are depicted in a graphical format (Figures 12 through 17) because light data trends were similar for all 3 sites.

Point sample light levels were greatest and most variable in canopy gaps at both the shrub and herb layers (Table 4). A similar trend existed when point samples were averaged on a per gap basis (Table 5). Both point sample and gap-level light levels generally decreased, and were less variable, along the gradient from canopy gap to transition gap to closed canopy forest (Tables 4 and 5). Light intensities

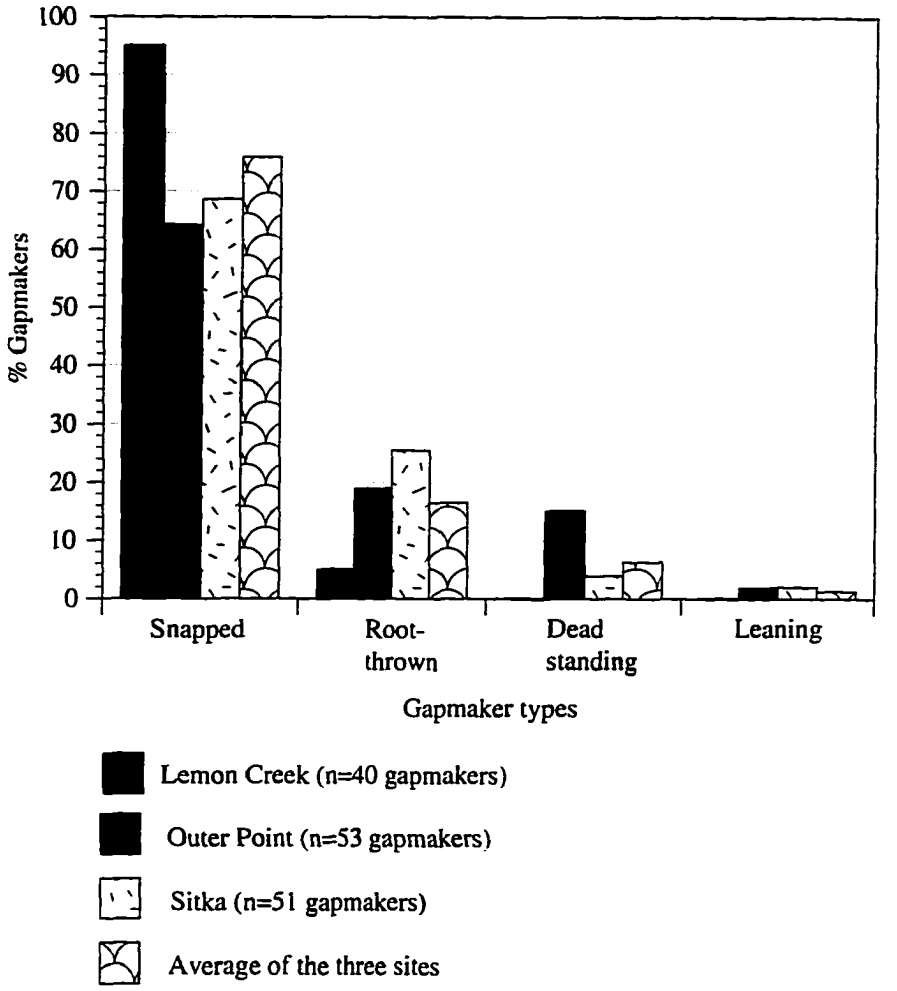

Figure 10. Proportions of gapmaker types.

Table 3. Gapmaker types from small-scale disturbances in selected forest systems.

		Gapmaker Type (%)							
Forest type [1]	Region	DS [2]	Sn [3]	Rt [4]	Part Rt [5]	Ln [6]	Br Br [7]	Other	Source
Tsuga	Alaska		99	1					Hocker 1990
			87	13					
			95	5					This study (Lemon Creek)
		15.1	64.2	18.9		1.9			This study (Outer Point)
		3.9	68.6	25.5		2			This study (Sitka)
		6.3	75.9	16.5		1.3			This study (mean value)
Picea-Tsuga	Oregon	4	84	12					Taylor 1990
Abies-Tsuga-Chamaecyparis	British Columbia	55	31	13					Lertzman and Krebs 1991 (4 sites)
Acer-Fagus	Ohio		53.3	28.9			17.8		Runkle 1990
Cove hardwoods	Tennessee	3	87	10					Barden 1981
Mesic (mixed species)	Eastern North America	10	58	14	6		13		Runkle 1982 (14 sites)
Pinus-Quercus	Mexico	26.4	39.5	20.5				0.9	Arriaga 1988
Amomyrtus-Laurelia	Chile		27	64					Armesto and Fuentes 1988
Nothofagus	Patagonia		19.4	80.6					Veblen 1989
			24.3	75.7					

[1] Forest type was classified by genus names of dominant overstory tree species when possible.
[2] DS = Dead standing
[3] Sn = Snapped
[4] Rt = Root-thrown
[5] Part Rt = Partly root-thrown
[6] Ln = Leaning
[7] Br Br = Broken branches

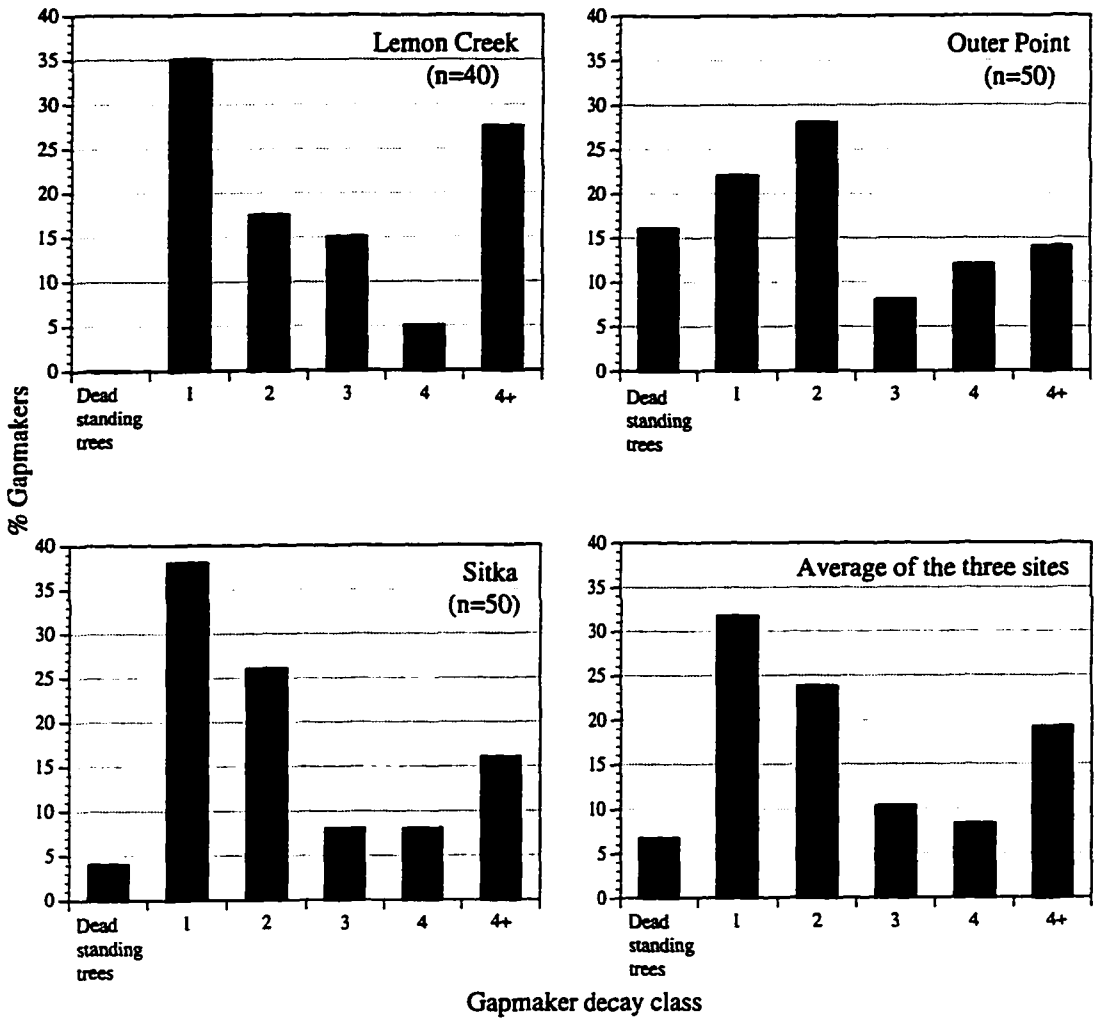

Figure 11. Frequency distributions of gapmakers by decay class.

Table 4. Characteristics of point sample diffuse light above shrub and herb layers. Diffuse light levels are expressed as % of diffuse sunlight in the open for 3 forest positions.

		Canopy gap		Transition gap		Closed canopy forest	
Site		Shrub layer	Herb layer	Shrub layer	Herb layer	Shrub layer	Herb layer
Lemon Creek	Mean	8.6	5.3	6.9	4.9	4.6	4
	SD	3.8	3.5	2.6	2.7	1.5	1.5
	Median	8	4.6	6.2	4.6	4.3	3.9
	n	265	265	333	333	135	135
Outer Point	Mean	10	3.2	7.3	3.2	7.2	3.2
	SD	5.6	2.5	3.5	2	3.4	2
	Median	10.5	2.4	6.4	2.6	6	2.6
	n	189	137	184	124	124	124
Sitka	Mean	6.5	3.4	4.9	3	3.9	2.7
	SD	3	2.3	2.3	1.7	1.5	1.2
	Median	6.6	2.8	4.6	2.7	3.6	2.6
	n	227	227	282	282	88	88

Table 5. Characteristics of average gap-level diffuse light above shrub and herb layers. Diffuse light is expressed as % of diffuse sunlight in the open for 2 forest positions. Average light level was determined from a minimum of 5 samples within a gap type.

		Canopy gap		Transition gap	
Site		Shrub layer	Herb layer	Shrub layer	Herb layer
Lemon Creek	Mean	8.1	5.1	7.2	5.1
	SD	3.1	2.4	2	1.9
	Median	7.8	4.5	7	4.6
	n	19	19	19	19
Outer Point	Mean	9.9	3.5	7.6	3.3
	SD	2	1.6	2.6	1.3
	Median	9.9	3.4	7.5	2.6
	n	12	8	15	9
Sitka	Mean	9	5.9	4.9	3.1
	SD	5.3	5.6	1.6	1.1
	Median	9	4	4.9	3.1
	n	8	8	17	17

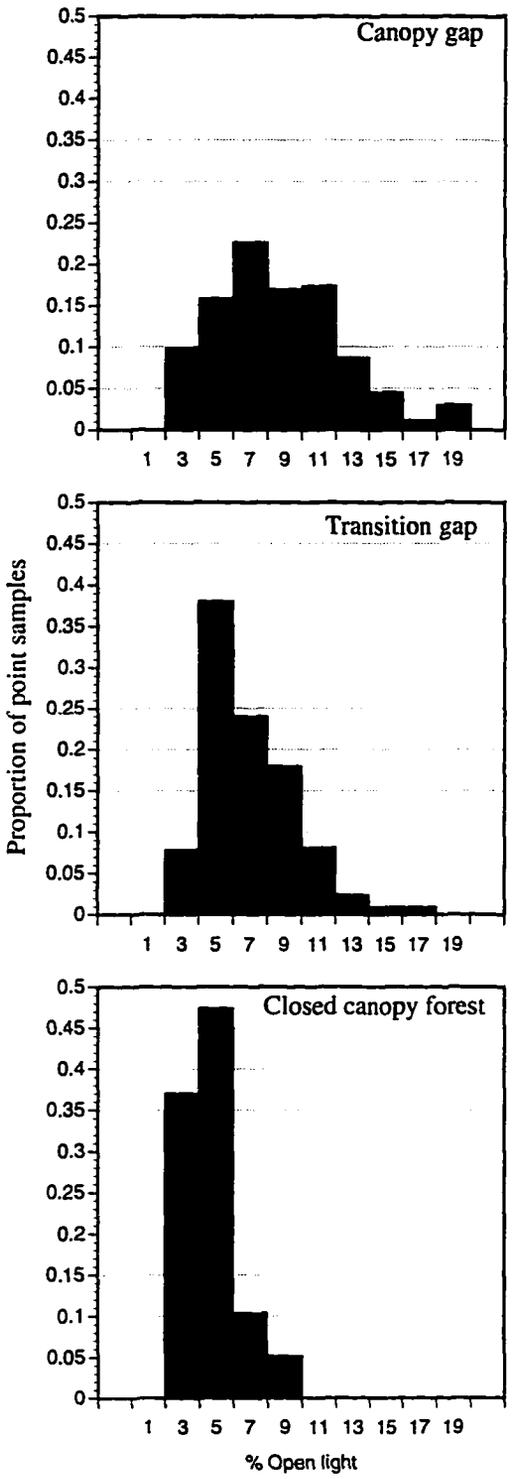

Figure 12. Frequency distributions of point sample shrub layer diffuse light levels. Histograms are for point samples in 3 forest positions at the Lemon Creek site. Light level classes represent 1.9% intervals (e.g. the 1% light class includes light levels from 0-1.9%).

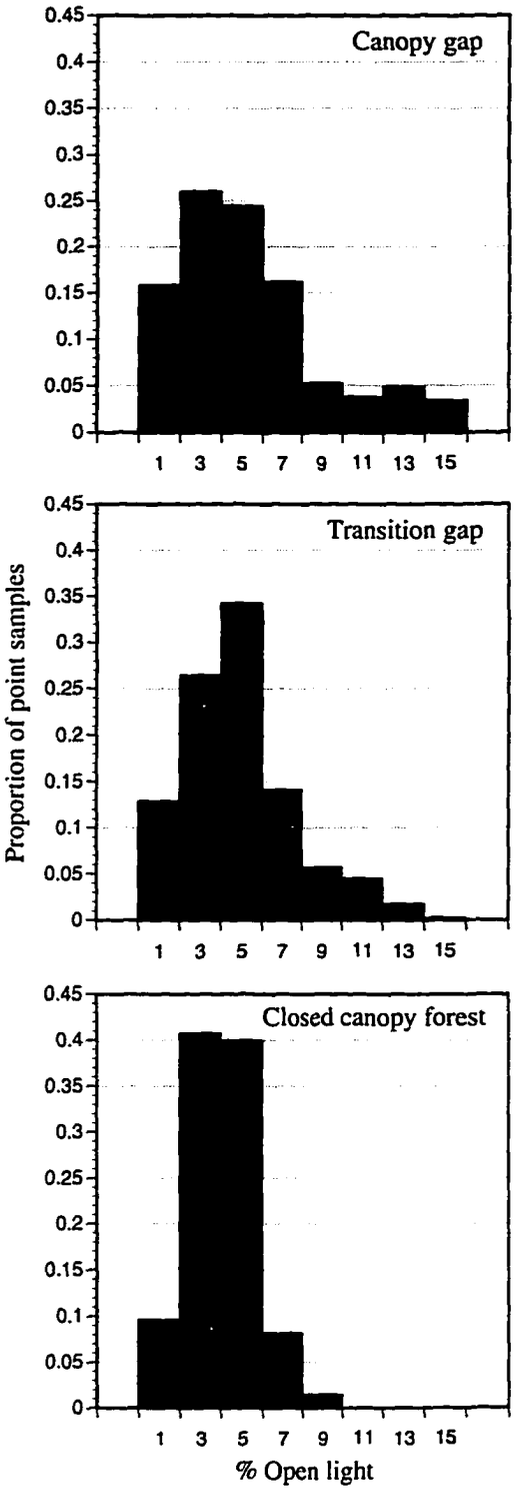

Figure 13. Frequency distributions of point sample herb layer diffuse light levels. Histograms are for point samples in 3 forest positions at the Lemon Creek site. Light level classes represent 1.9% intervals (e.g. the 1% light class includes light levels from 0-1.9%).

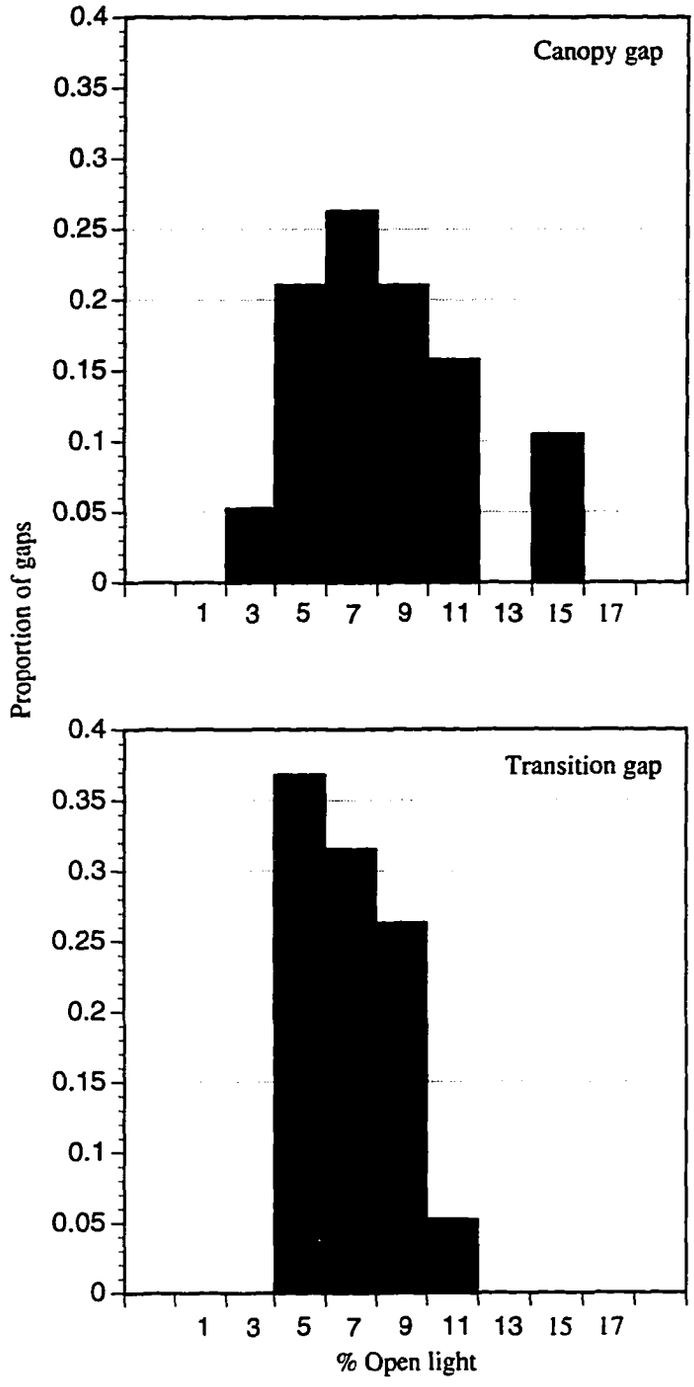

Figure 14. Frequency distributions of gap-level shrub layer diffuse light. Light readings were averaged on a per gap basis in 2 forest positions at the Lemon Creek site. Average light level was based on a minimum of 5 samples within a gap type. Light level classes represent 1.9% intervals (e.g. the 1% light class includes light levels from 0-1.9%).

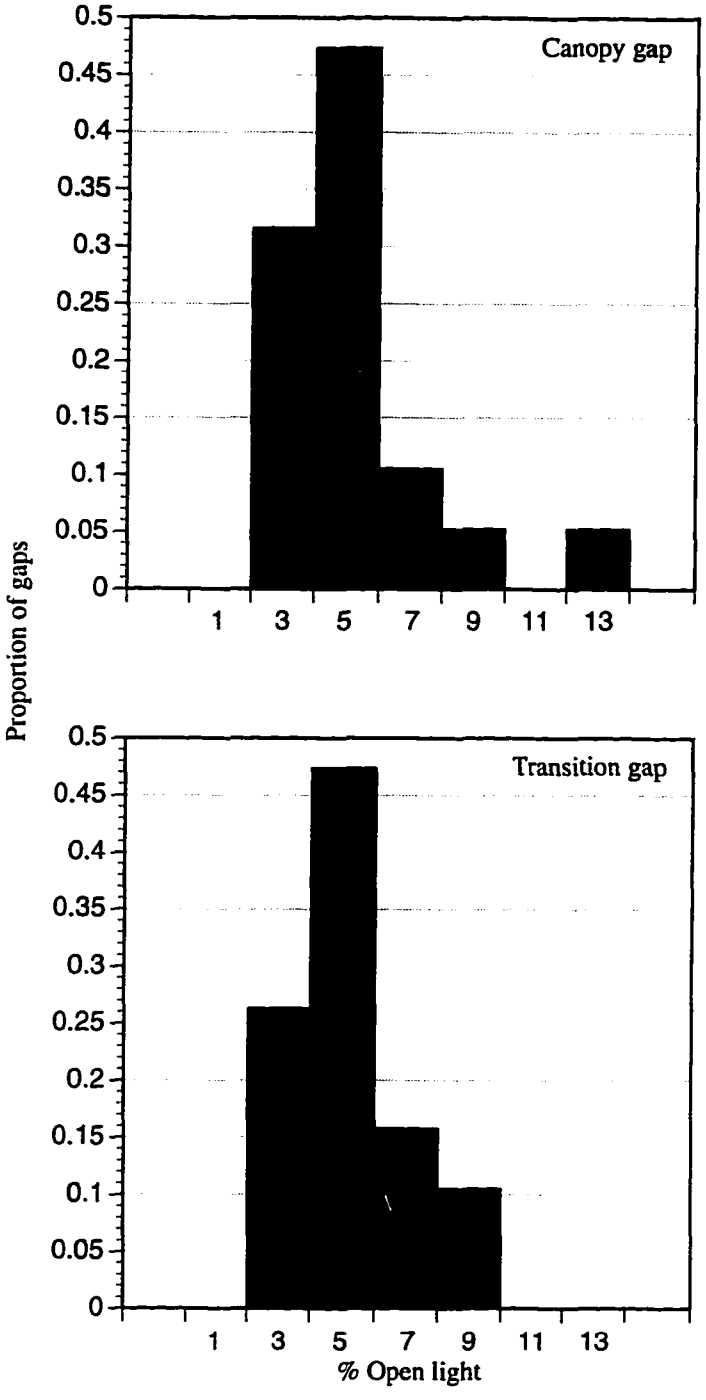

Figure 15. Frequency distributions of gap-level herb layer diffuse light. Light readings were averaged on a per gap basis in 2 forest positions at the Lemon Creek site. Average lightlevel was based on a minimum of 5 samples within a gap type. Light level classes represent 1.9% intervals (e.g. the 1% light class includes light levels from 0-1.9%).

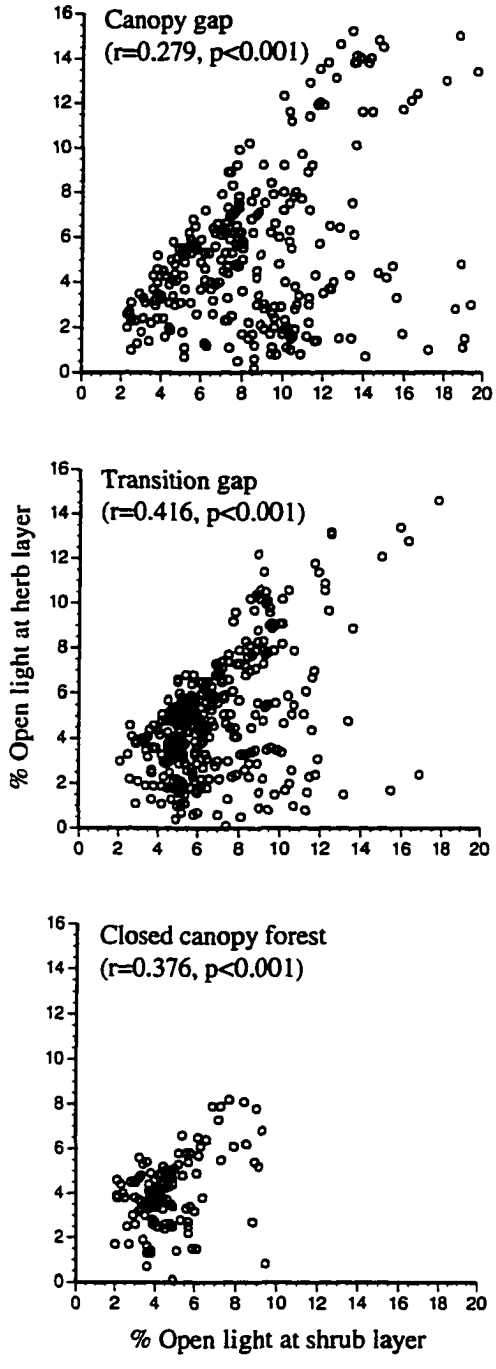

Figure 16. Point sample herb layer light compared to shrub layer light. Data are diffuse light readings in 3 forest positions at the Lemon Creek site. Spearman rank correlation coefficients are shown.

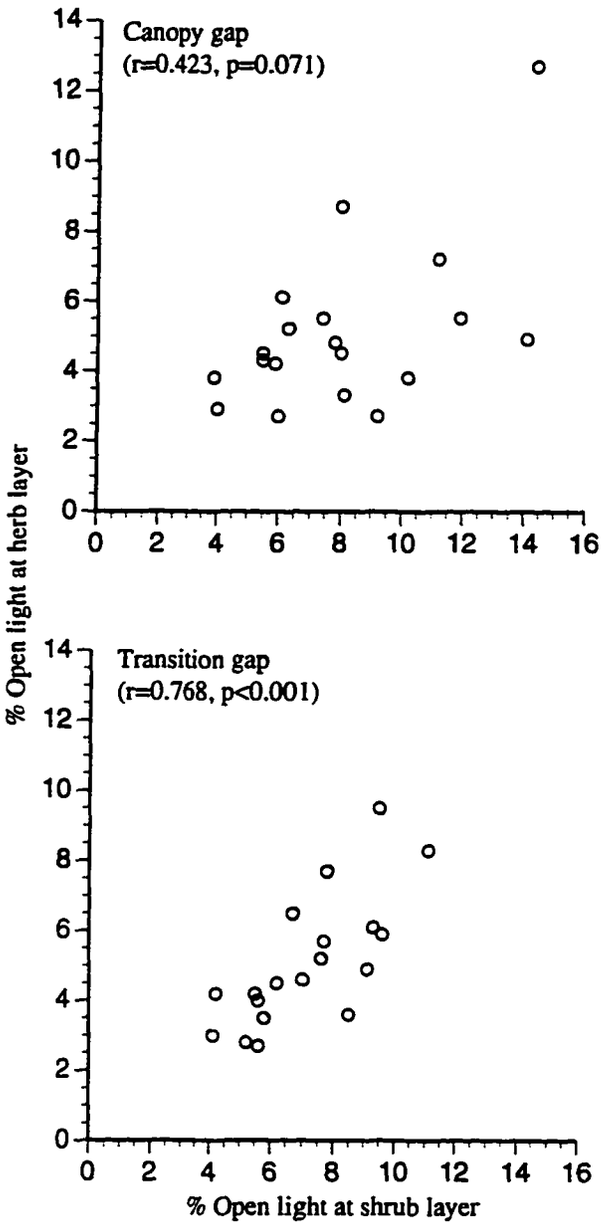

Figure 17. Gap-level herb layer light compared to shrub layer light. Data are diffuse light readings averaged on a per gap basis in 2 forest positions at the Lemon Creek site. Average light level was based on a minimum of 5 samples within a gap type. Spearman rank correlation coefficients are shown.

generally had a 1-tailed distribution and were concentrated at lower levels. This trend existed for point samples and average light intensities, at both the shrub and herb layers (e.g. Figures 12 through 15).

Light interception by shrub layer plants resulted in a decrease in light levels at the herb layer for point samples (Table 4) as well as for gap-level averages (Table 5). The reduction in point sample light levels from the shrub to the herb layer was largest in canopy gaps and least under closed canopy forest. The same trend existed for gap-level light intensities with the reduction of light intensity from shrub to herb layer being greater in canopy gaps than in transition gaps. At a given site, average herb layer light levels were similar across the gradient from canopy gaps to closed canopy forest for point samples (Table 4). Differences in average herb layer light levels from canopy gaps to transition gaps for gap-level averages were similar at 2 of the 3 sites as well (Table 5).

However, the relationship between shrub layer and herb layer radiation levels were not always strong or consistent. The relationship of point sample herb layer light and shrub layer light was not strongly correlated ($r < 0.50$) at the 3 sites (e.g. Figure 16). The relationship of mean herb layer light and shrub layer light was not consistent. Mean herb layer light and shrub layer light were not strongly correlated in canopy gaps at Lemon Creek (Figure 17) or Outer Point, but they were significantly correlated at Sitka ($r = 0.644$, $p = 0.007$). Mean herb layer light and shrub layer light were significantly correlated in transition gaps at Lemon Creek ($r = 0.768$, $p < 0.001$, Figure 17) and Sitka ($r = 0.784$, $p < 0.001$) but not at Outer Point.

Point sample shrub layer light levels were largest at Outer Point and smallest at Sitka in all 3 forest positions (Table 4). This pattern corresponds to mean and

median canopy gap areas for the sites, with Outer Point having the largest canopy gaps and Sitka having the smallest ones (Table 2). However, the same association of light intensity and canopy gap area did not exist for herb layer light levels.

Differences in point sample mean light level between the shrub and herb layers corresponded to mean canopy gap size in both canopy and transition gaps (expanded gap area minus canopy gap area; Table 2). Outer Point showed the greatest reduction in mean light intensity of point samples from the shrub to the herb layer, and Sitka showed the smallest reduction (Table 4). The same trend was observed for gap-level mean light values in transition gaps. Differences in mean light levels between shrub and herb layers for gap-level averages in canopy gaps were again greatest at Outer Point, but least at Lemon Creek (Table 5). However, the difference between Lemon Creek and Sitka was 0.1%, and easily within the range of measurement error. However, no significant correlations were found between canopy or transition gap areas and mean gap-level shrub light values in canopy and transition gaps.

Species Richness, Cover, and Height

No significant relationships were found between plant species richness and gap area (canopy gap and transition gap). Also, significant relationships did not exist between species richness and shrub and herb light levels at the scale of 1 m^2 across the gradient from canopy gap to closed canopy forest. No significant relationships were found between individual plant species (or groups of species such as all ferns) cover at the scale of 1 m^2 and shrub and herb light levels across the gradient from canopy gap to closed canopy forest. The only significant relationships that were identified were between plant species (or group of species) cover expressed as a % of

the total area of a gap that was sampled (gap-level species cover) and mean light intensity at the gap level (canopy or transition gap) (Table 6). However, these relationships were not consistent among sites, species, or positive/negative nature of the correlations.

The influence of gaps on plant species occurrence appears to be variable, depending upon the species and the site (Table 7). Percent occurrence of the majority of species does not increase or decrease along the gradient from canopy gap to closed canopy forest in a consistent fashion across all 3 sites. However, branched twistedstalk (*Streptopus amplexifolium*) consistently occurred more often in canopy or transition gaps at all sites. Deer fern (*Blechnum spicant*), only found at the Sitka site, occurred in much greater abundance in gaps. Some of the least common species, such as Pacific red elder (*Sambucus racemosa*), trailing black currant (*Ribes laxiflorum*), forest starwort (*Stellaria crispa*), heart-leaved twayblade (*Listera cordata*), baneberry (*Actaea rubra*), and sweet-scented bedstraw (*Galium triflorum*), were found only in a gap position. Conversely, licorice fern (*Polypodium glycyrrhiza*) was only found under closed canopy forest.

Beta-diversity, calculated using the Sorenson Index (C_s) for qualitative data (Magurran 1988), was smallest when comparing canopy gaps and closed canopy forest for all 3 sites (Table 8). However, C_s was relatively large for all 2-way comparisons of forest positions at all sites; C_s ranged from 0.833 to 0.952.

No significant correlations were found between light levels at the shrub layer and the height of the tallest individual of each woody species rooted in the 1 m^2 understory vegetation plots. However, some relationships existed between the mean and median heights of woody species and forest position (Table 9). Mean and

Table 6. Significant [1] correlations for gap-level light compared to plant species cover [2]. Spearman rank correlation was used to compare mean diffuse light levels within a gap type to individual plant species cover and combined plant cover for groups of plant species (e.g. ferns, forbs). Correlations were calculated for all plant species, but only significant correlations are shown. Average light level was determined from a minimum of 5 samples within a gap type or for a light stratum. See Table 7 for scientific names of plant species.

Site	Gap type [3]	n	Light stratum	Species (individuals/groups)	r [4]
Lemon Creek	CG	14	Shrub	Pacific red elder	0.508
		14	Herb	Short twistedstalk	0.650*
				Fern layer total	0.541*
				Oak fern	0.646*
				Forb layer total	0.607
	TG	19	Herb	Five-leaf bramble	0.551*
				Single delight	0.589*
Outer Point	CG	12	Shrub	Western hemlock/ Sitka spruce seedling total	0.596*
				Blueberry	-0.546
		8	Herb	Shrub layer total	-0.714*
				Herb layer total	0.643
				Blueberry	-0.643
				Bunchberry	0.905*
				Five-leaf bramble	0.810*
				Lady fern	0.639
Outer Point	TG	14	Shrub	Blueberry	-0.517
		8	Herb	Blueberry	-0.952*
				Fern-leaf goldthread	-0.830*
				Five-leaf bramble	0.724*
				Lady fern	0.699
Sitka	CG	14	Shrub	Five-leaf bramble	-0.560*
		14	Herb	Moss stratum total	-0.514
				Tall twisted stalk	-0.595*
				Deer fern	-0.721*
	TG	16	Shrub	Single delight	0.527*
		16	Herb	Herb stratum total	0.560*
				Foam flower	0.545*

[1] Significant correlation coefficients had $r > 0.50$ and a $p < 0.10$.

[2] Plant species (or group of species) cover expressed as a % of the total area of a gap that was sampled.

[3] CG = canopy gap, TG = transition gap

[4] $P < 0.05$ indicated by *.

Table 7. Percent occurrence of understory plant species in 3 forest stands. Species occurrence was based upon absence or presence within 1 m^2 plots in canopy gaps (CG), transition gaps (TG), and under closed canopy forest (FC). Sample sizes are indicated in parentheses.

			Lemon Creek			Outer Point			Sitka		
			CG	TG	FC	CG	TG	FC	CG	TG	FC
Life form	Scientific name	Common name	(144)	(185)	(70)	(150)	(148)	(64)	(144)	(173)	(52)
Tree	*Tsuga heterophylla*	Western hemlock	50.0	46.0	65.7	62.0	52.7	60.9	86.8	90.8	92.3
	Picea sitchensis	Sitka spruce	4.2	2.7	5.7	21.3	12.2	12.5	11.8	12.7	21.2
Tall shrub	*Vaccinium alaskaense/ovalifoliun*	Alaska/early blueberry	91.7	81.7	95.7	86.7	89.2	76.6	26.4	28.9	15.4
	Menziesia ferruginea	Rusty menziesia	8.3	14.1	14.3	43.3	49.3	42.2	22.9	26.6	13.5
	Oplopanax horridum	Devil's club	3.5	4.9	2.9	28.0	21.0	21.9	25.7	12.7	28.8
	Vaccinium parviflorum	Red huckleberry		0.5	1.4	0.7	0.7	1.6	28.5	34.7	40.4
	Rubus spectabilis	Salmonberry		0.5	1.4		0.7	1.6	24.3	20.2	36.5
	Sambucus racemosa	Pacific red elder	2.8	1.1				3.1	0.7		
	Ribes laxiflorum	Trailing black currant		1.1		0.7	2.0				
Forb/short woody	*Rubus pedatus*	Five-leaf bramble	92.4	91.4	90.0	85.3	87.8	79.7	6.3	11.6	15.4
species	*Cornus canadensis*	Bunchberry	64.6	68.7	74.3	75.3	75.7	81.3	10.4	13.3	7.7
	Streptopus streptopoides	Short twistedstalk	71.6	78.4	87.1	38.0	35.1	39.1	21.5	23.7	17.3
	Coptis asplenifolia	Fern-leaf goldthread	84.0	85.4	82.9	48.7	40.5	50.0	4.9	5.2	5.8
	Moneses uniflora	Single delight	18.1	21.6	37.1	22.7	25.7	32.8	50.7	59.0	67.3
	Maianthemum dilitatum	False lilly-of-the-valley	4.2	4.3	7.1	32.7	36.5	48.4	51.4	55.5	55.8
	Tiarella trifoliata	Foam flower	7.6	6.0		22.7	20.3	23.4	21.5	11.6	15.4
	Streptopus amplexifolium	Branched twistedstalk	7.6	6.0	5.7	6.7	6.7	3.1	4.9	7.5	5.8

Table 7 continued

			Lemon Creek			Outer Point			Sitka		
			CG	TG	FC	CG	TG	FC	CG	TG	FC
Life form	Scientific name	Common name	(144)	(185)	(70)	(150)	(148)	(64)	(144)	(173)	(52)
Forb/short woody	*Circaea alpina*	Enchanter's-nightshade				7.3	5.4	14.1			
species	*Lysichiton americanum*	Skunk cabbage	0.7			5.3	10.1	6.3	0.7	0.6	1.9
	Unknown grass/sedge	Grass/sedge						1.6	2.1		
	Stellaria crispa	Forest starwort				2.7					
	Streptopus roseus	Rosy twistedstalk				0.7		1.6			
	Prenanthes alata	Rattlesnake root					0.7	1.6			
	Listera cordata	Heart-leaved twayblade		0.5					0.7		
	Actaea rubra	Baneberry					0.7				
	Galium triflorum	Sweet-scented bedstraw				0.7					
Fern	*Dryopteris austriaca*	Shield fern	87.5	83.2	88.6	56.0	47.3	39.1	64.6	53.2	57.7
	Gymnocarpium dryopteris	Oak fern	6.9	4.9	10.0	63.3	58.8	51.6	34.0	23.7	21.2
	Athyrium felix-feminia	Lady fern	1.4	0.5		6.0	5.4	12.5	2.8	2.3	3.8
	Blechnum spicant	Deer fern							20.8	11.6	1.9
	Thelypteris phegopteris	Beech fern						6.3	1.4	0.6	
	Polypodium glycyrrhiza	Licorice fern									1.9

Table 8. Qualitative Sorenson Index values comparing plant richness in 3 forest positions. This index was used to determine the similarity of plant species richness in canopy gaps (CG), transition gaps (TG), and closed canopy forests (FC) at 3 sites.

Forest positions being compared	Lemon Creek	Outer Point	Sitka
CG/TG	0.923	0.870	0.933
TG/FC	0.865	0.875	0.952
CG/FC	0.824	0.833	0.889

Table 9. Heights of woody plant species in 3 forest positions. Summary statistics are shown for the tallest individuals of each woody species in the shrub stratum[1] rooted within 1-m^2 plots in three forest positions. Species with <10 measured individuals in a forest position are not shown.

		Canopy gaps			Transition gaps			Under forest canopy		
Species	Site[2]	$\bar{x}$ ± SD	Median	n	$\bar{x}$ ± SD	Median	n	$\bar{x}$ ± SD	Median	n
Western hemlock	LC	23.0 + 35.2	8.5	62	13.1 + 20.5	5.0	77	9.4 + 15.1	4	45
	OP	49.1 + 57.9	28.5	82	37.9 + 58.6	20.0	71	30.5 + 25.4	24	34
	S	45.3 + 43.5	33.0	112	36.1 + 31.8	24.0	150	28.1 + 24	20	48
Sitka spruce	OP	29.9 + 43.4	12.0	31	18.1 + 12.9	18.0	15			
	S	15.6 + 23.5	10.0	10	32.5 + 64.8	10.0	20	12.6 + 19.3	5	11
Blueberry	LC	61.0 + 27.6	60.0	80	58.6 + 32.5	53.0	93	54.7 + 29.7	43.5	46
	OP	78.7 + 36.3	81.5	94	89.4 + 41.7	91.0	90	98.3 + 39.5	97	40
	S	68.3 + 27.4	63.5	12	71.2 + 38.6	64.0	26			

Table 9 continued

Species	Site [2]	Canopy gaps $\bar{x} \pm SD$	Canopy gaps Median	Canopy gaps n	Transition gaps $\bar{x} \pm SD$	Transition gaps Median	Transition gaps n	Under forest canopy $\bar{x} \pm SD$	Under forest canopy Median	Under forest canopy n
Rusty menziesia	OP	89.7 + 68.1	95.0	22	101.9 + 87.5	89.0	28	145.8 + 98.1	140	12
	S	54.9 + 71.5	22.5	18	39.0 + 57.2	11.5	26			
Red huckleberry	S	85.9 + 41.9	86.0	22	75.2 + 40.2	72.0	29	92.8 + 44.5	88	13
Salmonberry	S	54.8 + 72.2	26.0	12	17.8 + 48.5	2.0	11	4 + 8.5	2	17
Devil's club	OP	133.0 + 94.3	115.0	10						
	S	42.8 + 42.4	40.0	10						

[1] Individuals of tree species with DBHs <2.5 cm were considered to be in the shrub stratum.

[2] Sites were: Lemon Creek (LC), Outer Point (OP), and Sitka (S).

median heights of western hemlock at all sites were largest in canopy gaps and smallest under closed canopy forests. This trend existed for some of the other woody species at some sites, but it was not consistent.

Tree Regeneration in Gaps

Seedling cover was significantly correlated with mean gap-level light only at Outer Point (Table 6).

Occurrence of western hemlock seedlings varied from 46.0 to 92.3% depending on site and forest position (Table 7). In contrast, Sitka spruce occurrence was substantially less; it occurred in 2.7 to 21.3% of the understory vegetation plots. Seedling occurrence was lowest at Lemon Creek. Regardless of forest position, western hemlock seedling occurrence was greatest at the Sitka site. The relationship of seedling occurrence and forest position was not consistent among the 3 sites.

As already mentioned, mean and median heights of western hemlock at all sites were largest in canopy gaps and smallest under closed canopy forests (Table 9). Also, mean and median heights of Sitka spruce seedlings were greater in canopy and transition gaps compared to those under closed canopy forest.

The great majority of gap trees and replacement trees (a subset of gap trees) were western hemlock at all sites. The proportion of gap trees comprised of Sitka spruce was: 1% at Lemon Creek, 5.2% at Outer Point, and 2.6% at Sitka. Sitka spruce replacement trees were only found at Outer Point (13.2%). All 3 sites had a small percentage of their population of live overstory trees comprised of Sitka spruce, but only Outer Point had a portion of its gapmaker population comprised of spruce (Table 10).

Table 10. Frequencies of Sitka spruce replacement trees, gapmakers, and live overstory trees. Sample sizes are in parentheses.

	% Sitka spruce		
	Replacement		Live overstory
Site	trees	Gapmakers [1]	trees [2]
Lemon Creek	0.0 (36)	0.0 (25)	2.0 (101)
Outer Point	13.2 (38)	11.6 (43)	5.8 (139)
Sitka	0.0 (21)	0.0 (40)	9.1 (121)

[1] Determined from gapmakers that were identifiable to species.

[2] Trees within five 0.1-ha reference plots with DBHs ≥ the minimum gapmaker DBH for the site.

DISCUSSION

Proportion of Land Area in Gaps

When compared worldwide, estimates of the amount of forest area in canopy and expanded gaps in the intensive study sites are generally within the range of estimates made in other forests (Table 1). However, estimates of the amount of land area in canopy gaps resulting from this study are less than those of other forests along the western coast of North America (Table 1).

The amount of forest area in canopy gaps in 2 forest complexes on Baranof Island was 2 to 3 times as great as the largest amount of forest area measured in the western hemlock/blueberry/shield fern plant association. The 2 forest complexes on Baranof Island occurred on loose Sitka volcanic ash on steep slopes, which may promote a high rate of tree turnover. These results suggest that the amount of area influenced by small-scale natural disturbances can vary greatly among plant associations.

Gap Characteristics

All disturbances encountered within the 3 intensive study sites during this study were small. No canopy gaps were too large to be sampled based on my criteria for defining the maximum size of a small-scale disturbance. Canopy gap characteristics generally were similar among sites; they were small even relative to the possible maximum size of a small-scale disturbance. The majority of canopy gaps were < 50 m^2 in area, had a D/H ratio < 0.50, and were created from the death of 1 or 2 gapmakers. These descriptors are closely related. A disturbance resulting from the death of only 1 or 2 gapmakers would have an area that is small in absolute terms.

The disturbance would also be small relative to the height of the surrounding forest when the height of the forest canopy is 30 to 40 m. The majority of canopy gaps also were multiple treefall gaps and experienced gap expansion.

The skewed frequency distribution of canopy gaps toward small areas observed in this study also has been observed in other studies (e.g. Krasny and Whitmore 1992, Cho and Boerner 1991, Lertzman and Krebs 1991, Stewart et al. 1991, Runkle 1990, Armesto and Fuentes 1988, Arriaga 1988, Foster and Reiners 1986, Runkle 1984). Mean and median area estimates of canopy and expanded gaps of the 3 sites were within the range of values estimated for forests in other regions of the world (Table 2).

Although D/H ratios provide an index of the functional role of gaps in the surrounding forest, this measure of canopy gap area or a similar measure such as gap aperture (Lawton and Putz 1988, Runkle 1992) is rarely measured. Average D/H ratios for the 3 sites in this study were very small and ranged between 0.20 and 0.29. Stewart et al. (1991) measured mean D/H ratios of 0.4 and 0.5 in 3 beech (*Nothofagus*) forests in New Zealand.

On average, the majority (52.6%) of canopy gaps on the 3 intensive study sites have experienced gap expansion. Gap expansion rates for these forests are not known. However, I was able to quantify 12 gap expansion events that occurred at Outer Point during the fall and winter of 1991-92. Canopy gap expansion ranged from 31 to 363% of the original canopy gap areas (i.e. pre-expansion gap areas). On average, canopy gap areas about doubled (109% increase) after the gap expansion events.

Gapmaker Characteristics

Identifying gapmakers types is important because different gapmaker types have different impacts on forest dynamics. Root-thrown gapmakers, and to a lesser extent leaning gapmakers, are the only ones that disturb and mix the soil. Some forest plant species may be able to grow only on this exposed soil. Dead standing gapmakers result from the gradual death of intact trees; they gradually relinquish their hold on resources such as space, nutrients, and light. However, root-thrown, leaning, and some snapped gapmakers are formed when a tree crown is quickly removed from the forest canopy. The rapid removal of a tree crown results in a sudden increase in the amount of resources available to other plants. It is reasonable to assume that plants respond differently to different patterns of increased resource levels.

The creation of such a large proportion of snapped gapmakers at Lemon Creek (95%) probably results because the majority of trees in the dominant and codominant forest canopy have internal decay and they are firmly rooted. During wind storms or snow-loading events, the trees probably break due to weakness in their boles before enough force is applied to result in displacement of their root systems.

Snapped gapmakers result from the collapse of dead standing gapmakers or snapping of live trees. Although the proportions of snapped gapmakers formed by these 2 mechanisms is unknown, results of a census of gapmakers created during the fall and winter of 1991-92 at Outer Point offer some insights. During the fall and winter of 1991-92, fifteen of the 27 (55.6%) new gapmakers, all western hemlock, were formed when live tree crowns were snapped. The other 12 (44.4%) gapmakers were root-thrown. The creation of all 27 gapmakers resulted from the death of living trees. Only 1 dead standing gapmaker collapsed during the same time period.

However, sampling may have been biased because locating gapmakers resulting from live tree death is easier than locating fallen trees dead for some time; fallen live trees present conspicuous green tree crowns on the forest floor. The lack of dead standing gapmakers at Lemon Creek suggests that snapped gapmakers at that site are created from live trees.

This ranking of the proportion of root-thrown gapmakers on the 3 sites appears to be related to wind exposure, site drainage, and structural integrity of the trees. The Sitka site is potentially exposed to more severe winter storms than the other 2 sites because it directly faces the Gulf of Alaska. The exposure to severe storm winds in conjunction with the presence of trees with little internal decay may explain why the Sitka site has the greatest percentage of root-thrown gapmakers, even though the site is well-drained. The Outer Point and Lemon Creek sites are exposed to destructive winds, but probably not to the same degree as the Sitka site. Outer Point is only moderately well-drained, possibly making trees more prone to uprooting than trees at the well-drained Lemon Creek site. As a whole, trees at Outer Point seem to have less internal decay relative to trees at Lemon Creek. The combination of poorer site drainage and the presence of trees with less internal decay may explain the greater proportion of root-thrown gapmakers at Outer Point compared to Lemon Creek.

Most root-thrown gapmakers are probably created from uprooting of live trees. All new root-thrown gapmakers (12) created during the winter of 1991-92 at Outer Point were live, solid trees with no indications of internal decay. However, not all trees are uprooted because of wind effects. For example, uprooting can occur on a calm day because of snowloading in conjunction with saturated soils. For this reason, I refer to individual fallen trees that have significantly displaced the root

system as "root-throws" (uprooting is also an appropriate term), and not "windthrows". Use of the term "windthrow" implies that wind was the disturbance agent; use of the term "root-throw" does not imply a causal agent of the disturbance event.

The relatively low percentage of dead standing gapmakers overall may be the result of the following scenarios:

1) Gapmakers are created most often from sudden death—snapping or root-throwing—of live trees whereas dead standing gapmakers result from gradual tree death. As previously mentioned, the 27 gapmakers created during the fall and winter of 1991-92 at the Outer Point study site resulted from the death of living trees. The probability of an internally weak, although still living, tree snapping because of snow-loading or wind stress is quite high. The majority of large trees at the Lemon Creek site have internal decay. This high incidence of decay probably explains why 95% of the gapmakers were snapped; no dead standing trees were present in the gaps that were sampled; and only 1 large, dead standing tree was observed in the entire study area. Internal decay was present in 6 of the 15 (40.0%) snapped gapmakers created from live trees during the winter of 1991-92 at Outer Point. Farr et al. (1976) determined that 35.3% of western hemlock, and 20.8% of Sitka spruce in southeast Alaska have decay indicators such as basal scars, trunk scars, frost cracks, broken tops, and fungus conks. Trees in the region also are highly susceptible to root-throwing because of the combination of shallow root systems, poorly drained soils, and high winds—usually during peak rain intensity (Alaback 1990). It is likely that in most cases, tree mortality occurs before a dead standing gapmaker is formed through senescence.

2) Dead standing gapmakers do not remain intact for very long and are rapidly converted to snapped gapmakers, so the probability of encountering them in a stand at any given moment is low. Hennon and Loopstra (1991) determined that 41 of 42 (97.6%) western hemlock trees had broken within 38 years of intentional girdling on Cat Island in southeast Alaska.

Proportions of gapmaker types from this study are compared to reported values of proportions of gapmaker types from other studies in Table 3. Snapped gapmakers were the most common gapmaker type in the other studies conducted in North America, with the exception of the study by Lertzman and Krebs (1991) where dead standing gapmakers were the most common. Root-thrown gapmaker were the most common in studies conducted in Chile and Patagonia.

Determining the proportion of gapmaker types by sampling at one point in time does not yield information about the dynamics of the creation of gapmakers (unless additional information about gapmaker age, such as decay class, is available). Comparison of the proportions of gapmaker types estimated from random line intersect sampling and the census of gapmakers created during the winters of 1991-92 and 1992-93 at Outer Point offers some insight. The proportions of snapped and root-thrown gapmakers were estimated to be 64.2 and 18.9% respectively when using line intersect sampling. The 1991-92 census yielded values of 55.6 and 44.4% respectively. If the values derived by line intersect sampling are assumed to be long-term average proportions of gapmaker types, then the proportion of snapped and root-thrown gapmakers created during the winter of 1991-92 was 87 and 235% respectively of the average proportion of snapped and root-thrown gapmakers created over a long period of time. Interestingly, no new snapped or root-thrown

gapmakers were formed during the winter of 1992-93. These results suggest: (1) year-to-year variability in the creation of different gapmaker types can be highly variable; and (2) sampling existing gapmakers of all ages, along with some measure of gapmaker age, is probably a better approach for understanding long-term gap dynamics.

The overall reduction of the number of gapmakers with increasing age from decay class 1 through 4 is probably the result of the infilling of canopy gaps over time. The < 20% (average) of gapmakers in decay classes 3 and 4 suggests that infilling of some canopy gaps, or older portions of them, results before gapmakers reach advanced stages of decay. Large logs (> 30 cm DBH) are decomposed to a stage of decay class 3 or greater in about 100 years after some large-scale wind-caused disturbances (Ott, unpubl. data). However, the minimum age at which a log enters the decay class 3 state of decay is unknown. These 2 observations allow the inference that most canopy gaps, or at least older portions of them, persist for up to 100 years if decay rates of logs in small-scale disturbances are similar to those in large-scale disturbances.

The presence of between 14 and 27.5% of decay class 4+ gapmakers also suggests that canopy gaps can persist for long periods of time. Some of these oldest canopy gaps had no small trees (DBH ≥ 2.5 cm). Other canopy gaps with decay class 4+ gapmakers had only small diameter gap-recruited or gap-released trees in them. Some of the oldest gaps did have larger diameter trees in them (e.g. up to 30.5 cm DBH), but the average height of the trees in the gap was less than the average height of the surrounding forest canopy (refer to the definition of a canopy gap). The lack of trees, or the presence of only small trees in these oldest canopy gaps suggests

that gap infilling rates can be very slow in some cases. Slow canopy gap infilling rates results in the persistence—and influence— of canopy gaps for long periods of time. This phenomenon represents a legacy effect of tree death in the forest canopy. The conventional concept of a canopy gap is that of a very transitory phenomenon; in reality canopy gap persistence can be highly variable.

The relatively large percentage of decay class 1 gapmakers at the Lemon Creek and Sitka study sites indicates a recent pulse of canopy gap formation and/or expansion at these sites. Decay class 1 logs persist for only a very short period of time— about 5 years after large-scale wind-caused disturbances (Ott, unpubl. data).

Wind Gradients

Individual characteristics of gaps and gapmakers were similar among the 3 sites as already discussed. However, a different picture emerges when some of the gap and gapmaker characteristics are viewed together. Three descriptors in particular appear to be indicative of the intensity of winds a site receives: (1) forest area in canopy gaps, (2) the proportion of multiple treefall gaps, and (3) the proportion of gap expansion events. The Lemon Creek site on the mainland had the least amount of forest area in canopy gaps, the least amount of multiple treefall gaps, and the smallest proportion of gaps that have experienced gap expansion. In contrast, the Sitka site facing the open Gulf of Alaska had the greatest amount of forest area in canopy gaps, the greatest number of multiple treefall gaps, and the most gaps that have experienced gap expansion.

The 3 intensive study sites appear to represent a gradient of exposure to severe fall and winter storms that usually blow from the southeast (Harris 1989). The

Lemon Creek site is protected from southeast gale winds. However, it is exposed to winds that originate in the Juneau icefield, and tree mortality occurs as a result of these winds (Chapter 3 of this thesis). The winds from the icefields apparently are less intense compared than southeast gales. Outer Point is influenced by southeast storm winds (Chapter 3 of this thesis), but it is probably partly protected by Douglas and Admiralty Islands (Figure 1). The Sitka site is fully exposed to southeast storm winds that blow into Sitka Sound from the Gulf of Alaska (Ott, unpubl. data; see Figure 1) and appears to experience the most intense winter storm winds.

Light Environment

Several factors may contribute to the concentration of low light microenvironments and relatively high variability in light intensities in canopy gaps. Sidelighting in tall-statured, high latitude forests such as those in southeast Alaska results in a very heterogeneous direct light environment as light filters through tree crowns and around boles of trees. Canopy gaps at the 3 sites are concentrated in small size classes both in absolute terms (Figure 5) and relative to the height of the surrounding forest (Figure 7). Therefore, I expect that sidelighting through intact forest surrounding canopy gaps can influence light microenvironments across even the largest canopy gaps that were sampled. Although I measured diffuse radiation levels, sidelighting may still be important.

Gap trees influence light microenvironments and probably contribute to the presence of some of the lowest light environments in canopy gaps. Shrub light readings were taken at a maximum height of 2 to 2.5 m. Height to diameter relationships of replacement trees at the 3 sites (Figure 18) indicate that the smallest

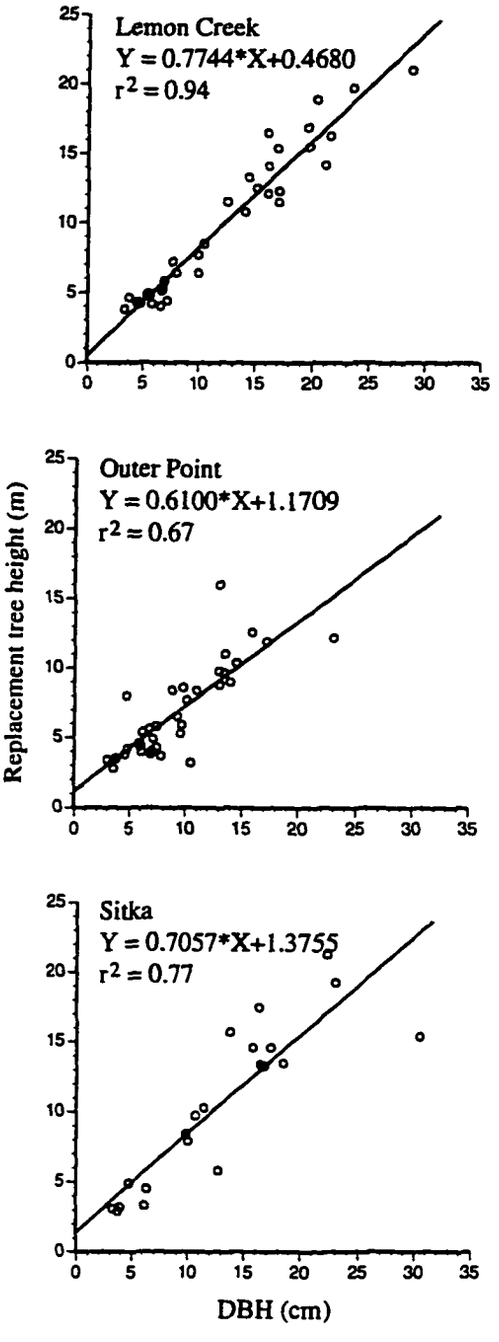

Figure 18. Relationships of height to diameter of replacement trees at 3 sites. Replacement trees included western hemlock and Sitka spruce.

diameter gap trees (2.5 cm DBH) were, on average, 2.4 to 3.1 m tall. Therefore, light microenvironments at the shrub and herb layers are expected to be under the influence of shading effects of gap trees that are directly overhead or that shade an area as a result of sidelighting. Gap-level average shrub light values were negatively correlated with gap tree density in, and between, both canopy and transition gaps at all 3 sites. Significant relationships existed between canopy gap tree densities and transition gap mean shrub light values at Lemon Creek ($r = -0.608$, $p = 0.006$), and between transition gap tree densities and transition gap mean shrub light at Sitka ($r = -0.512$, $p = 0.061$).

Light interception by shrub layer plants resulted in a decrease in light levels at the herb layer. Differential interception by shrub layer plants at different forest positions resulted in the greatest light interception occurring in the shrub layer in canopy gaps. The least amount of light interception by the shrub layer occurred under closed canopy forest for point samples and in transition gaps for gap-level averages. Shrub cover apparently was greatest in canopy gaps where light levels were greatest, thereby resulting in the greatest light interception in those environments. However, shrub layer vegetation is highly variable in density and spatial arrangement. A single measure of canopy cover does not indicate the nature of these characteristics. The variable nature of the shrub layer probably accounts for the fact that the relationship between shrub layer and herb layer diffuse light levels were not always strong or consistent.

Larger canopy gaps appeared to have higher overall light environments above the shrub layer. Shrub species could react to the increased light levels by increasing their leaf area index. Increased leaf area index of the shrub layer would increase light

interception at that layer, thereby resulting in a greater difference in light levels between shrub and herb layers as gap size increased.

However, no significant correlations were found between canopy and transition gap areas and mean gap-level shrub light values in the 2 forest positions. Three hypotheses may explain how shrubs can increase their leaf area index in gaps when no relationship exists between gap size and diffuse light levels. First, shrub cover may be more closely associated with the amount of direct sunlight an area receives and not strongly associated with diffuse radiation levels. Carbon accumulation associated with sunfleck activity can account for up to 65% of daily carbon gain in some understory plants (Chazdon and Pearcy 1991). Second, light may not be the limiting resource for biomass accumulation in plants in southeast Alaska. Canopy gap formation may result in the release of other, more limiting resources, in proportion to the size of the disturbances that are formed. Third, in forests where sidelighting has a significant influence on the total radiation budget, gap density, spatial arrangement of gaps, and gap orientation is expected to be more important than individual gap sizes. Overall light levels in a small canopy gap that lies north of a large canopy gap could potentially be as great or greater than light levels within the larger gap. At Outer Point, I have observed seedlings receiving direct radiation in a canopy gap as a result of sunlight entering a different canopy gap located to the south and then traveling under closed canopy forest for 20-30 m. Gap densities and spatial arrangements have not been closely examined in southeast Alaska.

Species Richness, Cover, and Height

Most species did not appear to be specialized to particular light environments within the range of observed diffuse light levels. Understory plant species in the 3 forests appear to be robust in terms of their light requirements compared to the range of light conditions present in the understory. However, some exceptions did occur. Of the more common species, deer fern and branched twistedstalk appear to favor gap environments. The species found in very low abundance that were only present in gaps are species that require higher light environments compared to the more common species.

The large Sorenson Index values indicate that gaps and closed canopy forest generally are very similar in species composition. Of the 3 forest positions, however, canopy gaps and closed canopy forest are the least similar.

The lack of a consistent relationship between shrub layer light levels and heights of the tallest individuals of woody species (with the exception of tree seedlings) may be a result of the robust sampling method used. Some woody individuals were tall enough to be in the shrub layer, some were short enough to be in the herb layer, and others fell somewhere in between the 2 vegetation layers. A more consistent relationship may have been found if shorter woody individuals were compared to herb layer light levels. However, the height of herb layer light readings was not recorded, and classifying the individuals that were taller than the herb layer but shorter than the shrub layer would have been arbitrary.

Regeneration in Gaps

Canopy gaps appear to influence understory tree dynamics. Western hemlock appears to benefit from the presence of canopy gaps. The high occurrence of hemlock both in gaps and under closed canopy forests suggests that hemlock is not a gap-dependent species for seed germination. Once established, western hemlock is very shade tolerant and can persist in a suppressed state for long periods of time. Height to age relationships of western hemlock seedlings at the 3 sites indicate that on average, 1m tall hemlock seedlings were 40 yrs. old (Figure 19). These numbers represent an average growth rate of 2.5 cm/yr. The fact that hemlock seedlings were tallest in canopy gaps at all 3 sites suggests that hemlock benefits from the overall increased light levels found in gaps once it becomes established. Alaback and Tappeiner (1991) found western hemlock height growth, number of branches, and biomass were linearly related to solar radiation transmission.

Sitka spruce occurred less frequently in the understory than western hemlock. The generally low light levels in both gaps and under forest canopy are probably below the threshhold necessary for successful establishment of this tree species. The greater heights of spruce in canopy and transition gaps suggests that, once established, it benefits from gaps. However, Sitka spruce appears to have the potential to maintain itself through gap-phase replacement only at Outer Point. This site has the largest mean and median gap areas and highest diffuse shrub light levels of the 3 sites. Taylor (1990) determined that Sitka spruce needed gaps of 800-1000 m^2 to persist in the coastal forests of the Pacific Northwest. It is generally accepted that Sitka spruce requires relatively large-scale disturbances because of its higher

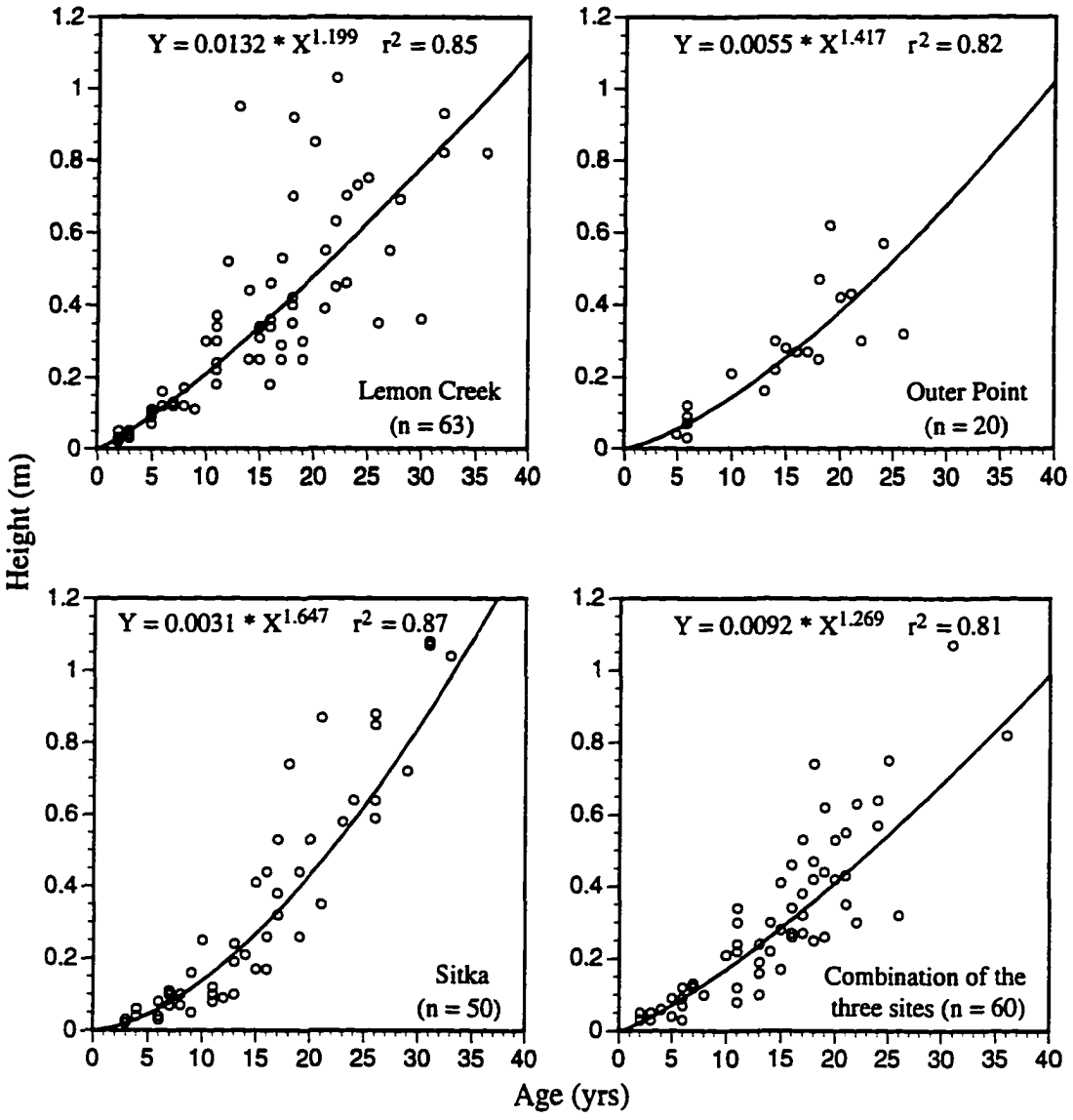

Figure 19. Relationships of height to age of western hemlock seedlings. Seedlings were randomly selected from those growing from organic rooting substrates and from the forest floor, located in both canopy gaps and under closed canopy forest. The graph depicting seedling growth of all 3 sites includes all 20 data points from Outer Point and 20 randomly selected points from both Lemon Creek and Sitka.

light requirements compared to western hemlock. The ability of spruce to maintain itself in a stand through gap-phase dynamics may be marginal at best.

The Role of Gaps in Forest Dynamics

Restricting one's view to results of this study alone would suggest that gaps do not play a major role in forest dynamics. No significant relationships were found between plant species richness and gap area or between species richness and light levels at the scale of 1 m^2. Plant cover was not consistently associated with light levels at the scale of 1 m^2 either. Few species appeared to be specialized to particular light environments within the range of observed diffuse light levels. However, established tree seedlings of spruce and hemlock appear to benefit from gaps, presumably because of the generally higher light levels associated with the disturbances.

A more significant influence of gaps on forest dynamics would have been detectable if larger spatial and temporal scales had been considered. Only forests with gaps were studied and gaps were treated as discrete, static entities.

Gaps occur in the old-growth stage of forest development described by Oliver (1981). According to Oliver's model, a forest that is initiated following a large-scale disturbance goes through 4 stages of development in the absence of additional major disturbances. The stand initiation stage represents the time during which new seedlings actively invade a site, and sprouting stems and advance regeneration begin or resume growth. The stem exclusion stage represents the time during which new stems are excluded from initiating and vertical stratification by species occurs in the existing stems because of intense competition for resources. The stem exclusion

stage usually begins upon canopy closure in light-limited forests. The understory reinitiation stage is the period when herbaceous and woody plants, including advance regeneration, begin to grow in the understory as the overstory becomes very mature. The old growth stage is the final stage of development when the overstory slowly breaks up (i.e. gaps are formed) and understory advance regeneration is locally released and moves into the overstory canopy.

By limiting the scope of this project to old-growth forests, more significant effects of canopy gaps were probably masked. Gaps comprise part of the fabric of old-growth forests. It is their creation that allows the development of structural and species diversity in the understory of a forest stand that was previously depauperate of both forms of diversity in the middle stages of forest development.

Treating gaps as discrete entities probably also resulted in the lack of consistent relationships among gaps, light, and forest understory vegetation. The effect of gaps on forest dynamics is probably cumulative. A particular point in the understory of a forest can be under the influence of several gaps simultaneously, especially in high latitude forests with a high degree of sidelighting. Gap density and spatial arrangement may have a greater influence than individual gap size on understory forest dynamics.

The variables measured during this study may have been inappropriate to detect consistent relationships among gaps and understory light and vegetation. For example, plant biomass or seedling densities may be better variables than leaf cover estimated in 10% increments for detecting those relationships.

Finally, information about gap age may be important for understanding relationships between forest overstory and understory dynamics. For example,

seedling density in Douglas-fir (*Pseudotsuga menziesii*) forests was found to correlate with gap age but not gap size (Spies et al. 1990). I was unable to reliably determine gap age because vegetation in a gap was sometimes responding to more than one disturbance.

Management Implications

Emulating patterns of small-scale natural disturbances probably would be best achieved if single tree selection and small group selection cuts were administered within a stand. Decision rules to determine how many trees to remove to create an "artificial gap" can be derived from canopy gap area distributions, distributions of D/H ratios, and the distribution of the number of gapmakers per gap. A decision rule based on the number of gapmakers per gap would be the easiest to administer on the ground.

A decision rule to determine where and when to remove harvest trees can be derived from the fact that (1) most gaps are multiple treefall gaps, and (2) an average of 57% of the multiple treefall gaps had gapmakers representing 2 or more decay classes. When stands are re-entered, most trees can be removed from the edges of existing "artificial gaps", and a smaller proportion of removals would come from the creation of new "artificial gaps". This action would attempt to emulate natural gap expansion and the natural initiation of new gaps. Re-entry times can only be suggested in very broad ranges based on the decay class distribution of gapmakers. The gapmaker age distribution has not been established at this point.

Emulating the amount of disturbance in gaps would mean that the cumulative removal of harvest trees over a reasonably long period of time would result in 5 to 15% of the land area being in "artificial gaps".

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CHAPTER 3

INTERPRETATION OF WIND AND TREEFALL PATTERNS AT THE SITE- AND LANDSCAPE-LEVEL IN THE FORESTS OF SOUTHEAST ALASKA: IMPORTANCE, TECHNIQUES, AND APPLICATION

Abstract. Understanding wind flows is important from both an ecological and management perspective. Wind disperses materials and is an important disturbance agent in forests throughout the world. A knowledge of wind direction and intensity allows silviculturists to make informed decisions regarding which silvicultural treatment(s) will result in minimal or at least acceptable wind damage in managed forest landscapes.

Treefalls result in coarse woody debris (CWD) which has numerous ecological functions in both terrestrial and aquatic ecosystems. The function of CWD is partly determined by its context in the local landscape. Wind partly determines the context of CWD in the local landscape by influencing treefall direction.

Techniques are needed that allow for interpretation of wind patterns in remote locations, at both site- and landscape-levels, and across complex topography. I demonstrate the use of circular data analysis as a technique to investigate the influence of topography, locally destructive winds, and their interaction on treefall direction at the site-level in the complex topography of southeast Alaska.

Using circular data analysis, I determined that the relationship between treefall direction and the direction of flow of destructive winds varied with tree size and topography. The direction of fall of trees that were previously growing in the overstory, such as gapmakers and large diameter root-throws, can be indicative of the direction of flow of destructive winds. However, care must be taken when inferring wind flow from treefall directions on steep slopes. Treefall directions of small diameter understory trees did not correspond to known wind flows.

I also demonstrate the feasibility of mapping wind flows across a large landscape (111,336 ha) of complex terrain in southeast Alaska using flagged trees, treefall directions of large-scale natural blowdowns, and treefall directions of blowdowns associated with clearcuts. Winds were found to flow both northward and southward across northeast Chichagof Island. The most damaging winds were from the south. Some areas of the peninsula were found to be more prone to wind damage than other areas.

INTRODUCTION

Importance of Understanding Wind Flows

The flow of wind across a landscape and its interaction with that landscape is important from both an ecological and management perspective. The ability of wind to disperse materials is one reason that understanding and predicting wind flows is important to ecologists, foresters, air quality managers, and other natural resource managers. Wind flows influence dispersal patterns of pollen, seeds, spores, small insects and arthropods, aerosols, and airborne particulates. Aerosols and airborne particulates can be classified as inert compounds, nutrients, or pollutants, depending on their interaction with the ecosystem or landscape of interest. Knowledge of wind fields is also important for modeling dispersion (Porch 1982), prospecting for sites suitable for harnessing wind energy (Hewson et al. 1977, Porch 1982), predicting the spread of wildfires (Holroyd 1970, Fosberg et al. 1976), and for locating ski runs—pockets of calm air being ideal (Holroyd 1970).

Knowledge of wind flows—and intensities—is also important for assessing the risk of wind damage to forests at both the site- and landscape-levels. A knowledge of wind direction and intensity allows silviculturists to make informed decisions regarding which silvicultural treatment(s) will result in minimal or at least acceptable wind damage to the surrounding forest or the residual stand (e.g. Hubert 1918, Weidman 1920, Behre 1921, Curtis 1943, Ruth and Yoder 1953, Alexander and Buell 1955, Gratkowski 1956, Alexander 1964, Gordon 1973, Harris 1989, Hånell and Ottosson-Löfvenius 1994). Specific silvicultural activities that benefit from this knowledge include:

1) Identification of harvest unit edges most prone to wind damage,

2) Determination of size and shape of harvest units,

3) Placement of harvest unit edges to minimize wind damage,

4) Identification of methods to salvage blowdown without further contributing to the problem, and

5) Assessment of riparian buffer strip stability (Steinblums et al. 1984).

Importance of Understanding Treefall Direction Patterns

Wind is an important disturbance agent, causing treefalls in forests throughout the world. Treefalls result in coarse woody debris (CWD), which has numerous ecological functions in both terrestrial and aquatic ecosystems. CWD serves as habitat for animals and plants, is important in nutrient cycling processes, and it has geomorphic functions (Harmon et al. 1986). Wind plays an important role in the functioning of CWD by influencing treefall direction.

The function of CWD is partly determined by its context in the local landscape. For example, the direction that a tree falls in relation to topography determines its influence on geomorphic processes (Harmon et al. 1986). CWD aligned along slope contours can function as a dam, slowing the flow of water and trapping detritus and soil, thereby reducing erosion (Maser et al. 1988). These debris dams may also contribute to micro-scale heterogeneity of both physical and chemical properties of the soil. Similarly the alignment of CWD in relation to streamflow within a riparian zone or in a water channel will influence the effect CWD has on water velocity, turbulence, and deposition of sediments and nutrients. Even CWD

outside an active water channel will influence streamflow characteristics during flood events.

Orientation of CWD also influences its function as habitat for animals and plants. For example, the accumulated humus and organic matter on the uphill side of CWD aligned parallel with the slope allows invertebrates and small vertebrates to tunnel alongside. The downhill side can provide shelter for larger vertebrates (Maser et al. 1988). CWD is important for tree regeneration and establishment in some forests (Thornburgh 1969, Quaye 1982, Christy and Mack 1984, Harmon et al. 1986, Harmon and Franklin 1989). Therefore, the spatial distribution of trees in these forests should partly be a function of treefall direction. Because spatial pattern is known to influence many ecologically important processes (Turner 1989), it seems reasonable to assume that the spatial distribution of trees will influence the function of the forests involved.

Methods of Studying Wind Flows and Treefall Directions

Understanding wind flows across large, complex landscapes or at remote sites can be difficult. Instrumentation is expensive and long-term data sets are usually only available at sparsely scattered weather stations—usually located in urban settings. Ecologists, natural resource managers, and others interested in wind flows and treefall patterns, need techniques to interpret wind patterns in remote locations, at both site- and landscape-levels, and across complex topography.

Treefall directions have been used to infer local patterns of destructive wind flow bordering clearcuts (Ruth and Yoder 1953, Gratkowski 1956, Alexander 1964,

Gordon 1973), and within intact forests (Henry and Swan 1974, Arriaga 1988, Foster 1988, Jonsson and Dynesius 1993).

Asymmetric growth of tree crowns has been used to interpret wind direction. Tree crowns that are flagged as a result of wind-training can be used to determine flows of prevailing winds that occur during the growing season (Lawrence 1939, Holroyd 1970). Wind-trained crowns develop when branches are bent because of exposure to a constant wind pressure from one direction during the growing season (Lawrence 1939, Holroyd 1970) when the tissues are most flexible (Lawrence 1939). Tree crowns that are flagged as a result of mechanical damage can be used to determine the direction of winter winds (Lawrence 1939, Holroyd 1970). Processes that result in a disproportionate amount of mechanical damage of crowns on the windward side are:

1) Pruning due to high wind pressures—sometimes accompanied by accumulation of glaze (Lawrence 1939),

2) Leaf and bud mortality due to ice scouring during strong winds (Lawrence 1939, Spurr and Barnes 1980), and

3) Tissue damage from salt spray carried by wind in coastal areas (Oosting 1956).

Asymmetric growth of tree trunks can be indicative of wind direction, with accelerated radial growth occurring on the lee side of conifers (Ruth and Yoder 1953, Bannan and Bindra 1970)—including buttressing (Ruth and Yoder 1953). However, trees growing on slopes—conifers at least—show accelerated growth on the downhill side of their trunks as well (pers. observ.). Also, buttressing of trees is not always associated with wind direction (Young and Perkocha 1994).

Compression failures in tree boles can be indicative of damaging wind direction. Compression failures show up as ridges or swellings on the leeward side of a tree. These failures result when the force imposed on a tree is large enough to cause compression failure on the lee side, but not so large as to cause tension failure on the windward side (Mergen and Winer 1952). Heavy snow loads can also result in compression failures (Mergen and Winer 1952).

The methods of studying wind and treefall direction described above have been used for the following purposes:

1) To investigate the interaction of wind and harvest unit edges, as well as damage to the stands adjacent to harvest units (Ruth and Yoder 1953, Gratkowski 1956, Alexander 1964, Gordon 1973);

2) To study damaging wind direction over time in a small area (Henry and Swan 1974);

3) To study treefall direction patterns as they relate to regional wind patterns at the site-level (e.g. Arriaga 1988, Jonsson and Dynesius 1993) and wind patterns of a specific wind event (e.g. Foster 1988); and

4) To map wind flows over small- to moderate-sized landscapes such as a watershed (e.g. Alexander and Buell 1955) or mountain top (e.g. Holroyd 1970).

However, these techniques have not been used to map wind patterns over large forested landscapes, especially over complex terrain. Also, I have not encountered the use of techniques to distinguish between the effects of wind and topography on treefall direction over complex terrain.

In this paper I demonstrate the feasibility of mapping wind flows across a large landscape of complex terrain using a combination of techniques. I have mapped the direction of both destructive winter winds and prevailing summer winds across approximately 111,293 ha of Chichagof Island in southeast Alaska. I also demonstrate the use of circular data analysis as a technique to investigate the influence of topography, locally destructive winds, and their interaction, on treefall direction at the site-level in the complex topography of southeast Alaska.

STUDY AREA

Geography and Climate

Southeast Alaska, also known as the Alexander Archipelago, is a region of complex topographic features—steep mountains, glaciers, fjords, straits, channels, wetlands, and coniferous forests. This region extends north to south 800 km and is about 160 km east to west. The majority of southeast Alaska lies within the boundaries of the Tongass National Forest.

Southeast Alaska has a cool, wet, maritime climate. Annual precipitation ranges between 150 and 500 cm (Harris et al. 1974), with at least 10% occurring during the summer months (Alaback 1991). Precipitation totals are generally heaviest on the outer coast and decline to the east until the eastern side of the innermost islands and the mainland are reached, where total precipitation increases again (Andersen 1955). Mean winter temperatures—December through February—generally decrease in a northwest direction, while mean growing season temperatures—May through September—generally decrease in a northerly direction (Andersen 1955). The July isotherm is $< 16^{\circ}$ C (Alaback 1991). Wind

patterns, ice fields, and other factors influence local rainfall and temperature patterns (Alaback 1982).

Three types of winds are primarily responsible for tree damage in southeast Alaskan forests: southeast gales, bora winds, and glacier winds. The strongest winds are most likely to occur in the fall and winter months (Harris 1989).

Southeast gales are the most damaging fall and winter winds that occur in southeast Alaska (Harris 1989). These storms are the result of low-pressure cells (i.e. cyclones) that have convergent, counterclockwise air flow in the Northern Hemisphere (Trewartha 1968, Schroeder and Buck 1977). Convergence results when there is a decrease in the horizontal area occupied by an air mass, resulting in surface winds that flow obliquely toward the center of a cyclone. Air flows obliquely toward the center of a cyclone because wind direction and speed are determined not only by the effects of the pressure gradient force, but also by the Coriolis force, friction, and centrifugal force (Trewartha 1968). Because the airstream is bounded by the earth's surface, convergence results in an upward movement of air as it flows toward the center of a low-pressure cell (Trewartha 1968). If sufficient moisture is present, precipitation results as the upward flowing air cools and condensation occurs (Schroeder and Buck 1977). Areas of low pressure and convergence zones are, therefore, characterized by thick clouds and abundant precipitation (Flohn 1969).

Most Pacific storms originate on the polar front over the relatively warm waters near Japan (Miller and Mantis 1947); this semi-permanent low-pressure system is called the Aleutian Low (Schroeder and Buck 1977). Overall, the portion of the Northern Hemisphere with the most frequent cyclonic activity is the Gulf of Alaska

(Klein 1957). The prevailing tracks of cyclones are generally farthest south in February, farthest north in August, and farther south in spring than in fall (Klein 1957). A normal storm tracks along the Aleutian Islands, the Alaska Peninsula, and all of the coastal areas of the Gulf of Alaska, thereby exposing these areas to a large majority of the storms crossing the north Pacific (Searby 1968).

Bora winds are a type of katabatic (i.e. downslope) wind that result from large pressure gradients and require a reservoir of cold air from an elevated interior (Reynolds 1980). Large-scale katabatic winds of this kind are called fall winds (Reynolds 1980); boras in southeast Alaska are called Taku winds. Boras are cold, dry winds that develop in places where steep mountains lie parallel to the coast (Reynolds 1980, Harris 1989); these winds are characteristically gusty and violent (Reynolds 1980). The presence of the mountains results in sharp climatic differences between relatively warm coastal areas and the cold interior of a continent. Boras develop when a strong pressure gradient exists between the coastal and interior areas, thereby forcing cold continental air to flow over the mountains and onto coastal areas. The pressure gradient is a result of either a deep low-pressure system over the coastal area or a high-pressure system over the interior (Harris 1989).

Glacier winds are smaller-scale (compared to bora winds) katabatic winds that result when cold air flows downslope from an elevated icefield (Harris 1989). The cold air results in a semi-permanent temperature inversion and cools the overlying air layer (Oke 1978). Glacier winds can be extremely gusty (Harris 1989).

Vegetation

About 57% of the land in southeast Alaska is forested, with the remaining area consisting of fresh water, non-forest land (e.g. alpine and wetland), and land developed for purposes other than timber production (USDA Forest Service 1990). Well-developed, closed-canopy forests are found from sea level to about 600 m in elevation. The hemlock-spruce forest type comprises the majority of closed-canopy forests in the region (Alaback 1982). At least 7 forest series achieve a late successional sere, and 3 of these are highly productive Sitka spruce (*Picea sitchensis*)-western hemlock (*Tsuga heterophylla)* associations: beach, riparian, and upland (Samson et al. 1989).

The temperate rainforest of southeast Alaska is characterized as having a high-frequency, low-intensity disturbance regime (Alaback 1990). The abundant year-round moisture and rarity of lightning storms result in minimal disturbance by fire (Harris 1989, Alaback 1990). However, this forest is highly susceptible to wind damage due to the combination of shallow root systems, poorly drained soils, and high winds—usually during peak rain intensity (Alaback 1990). Wind disturbance events typically are small-scaled and involve single trees or small groups of trees (Harris 1989, Alaback 1990, Chapter 2 of this thesis).

However, large-scale wind disturbances do occur. These disturbances can be classified as natural blowdowns that are not associated with human modifications of the landscape or as blowdowns associated with human activity, primarily timber harvesting.

Study Sites

Outer Point study site.—The Outer Point study site is located at the northwest tip of Douglas Island (Figures 20 and 21). It is about 8 ha in size and is bisected by a drainage that supports a western hemlock/blueberry/skunk cabbage (*Lysichiton americanum*) plant association (Martin et al. 1995). The area is fairly level with the slope ranging from zero to 7°.

Western hemlock dominates the Outer Point study site in all but the largest diameter classes; tree (DBH ≥ 2.5 cm) diameter distribution is bimodal (Figure 22). The age distribution of dominant and codominant trees also is bimodal, with the largest peak—22% of a 36 tree sample—in the 225 to 249 year age class, and a smaller peak—about 14% of the sample—occurring between 125 and 149 years. Ages of the dominant and codominant trees ranged from 106 to 331 years.

Lemon Creek study site.—The Lemon Creek study site is in the Lemon Creek drainage 10 km northwest of Juneau on the mainland (Figures 20 and 21). The site is about 11 ha in size. The aspect of the site is southeast to southwest and slope values range between zero and 34°.

Trees at the Lemon Creek site are comprised almost entirely of western hemlock (Figure 22). The oldest trees are probably 300 to 500 years old. The majority of the dominant and codominant trees have internal decay so their age distribution could not be determined. The diameter distribution of trees suggests that the forest is uneven-aged.

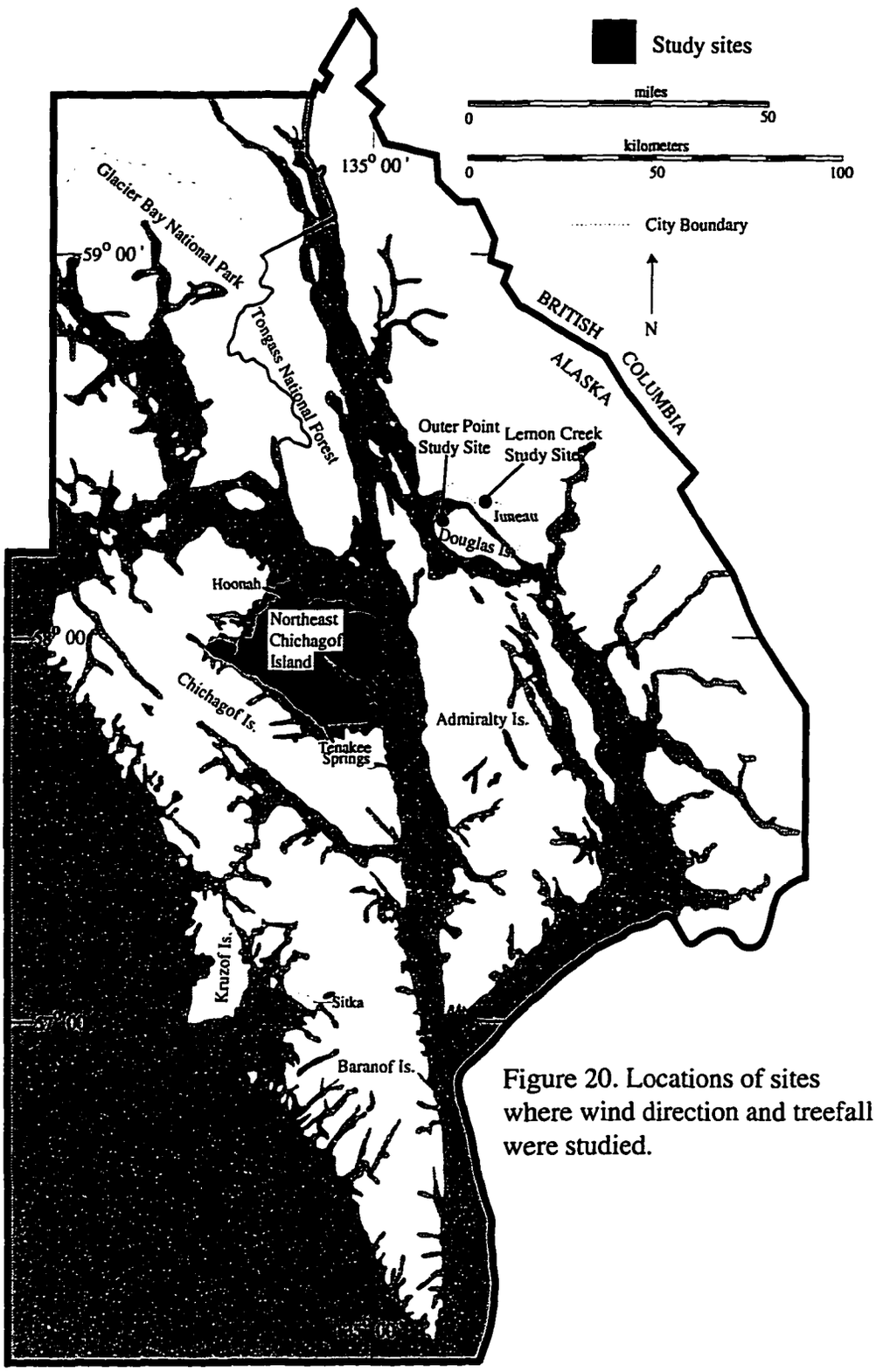


Figure 20. Locations of sites where wind direction and treefall were studied.

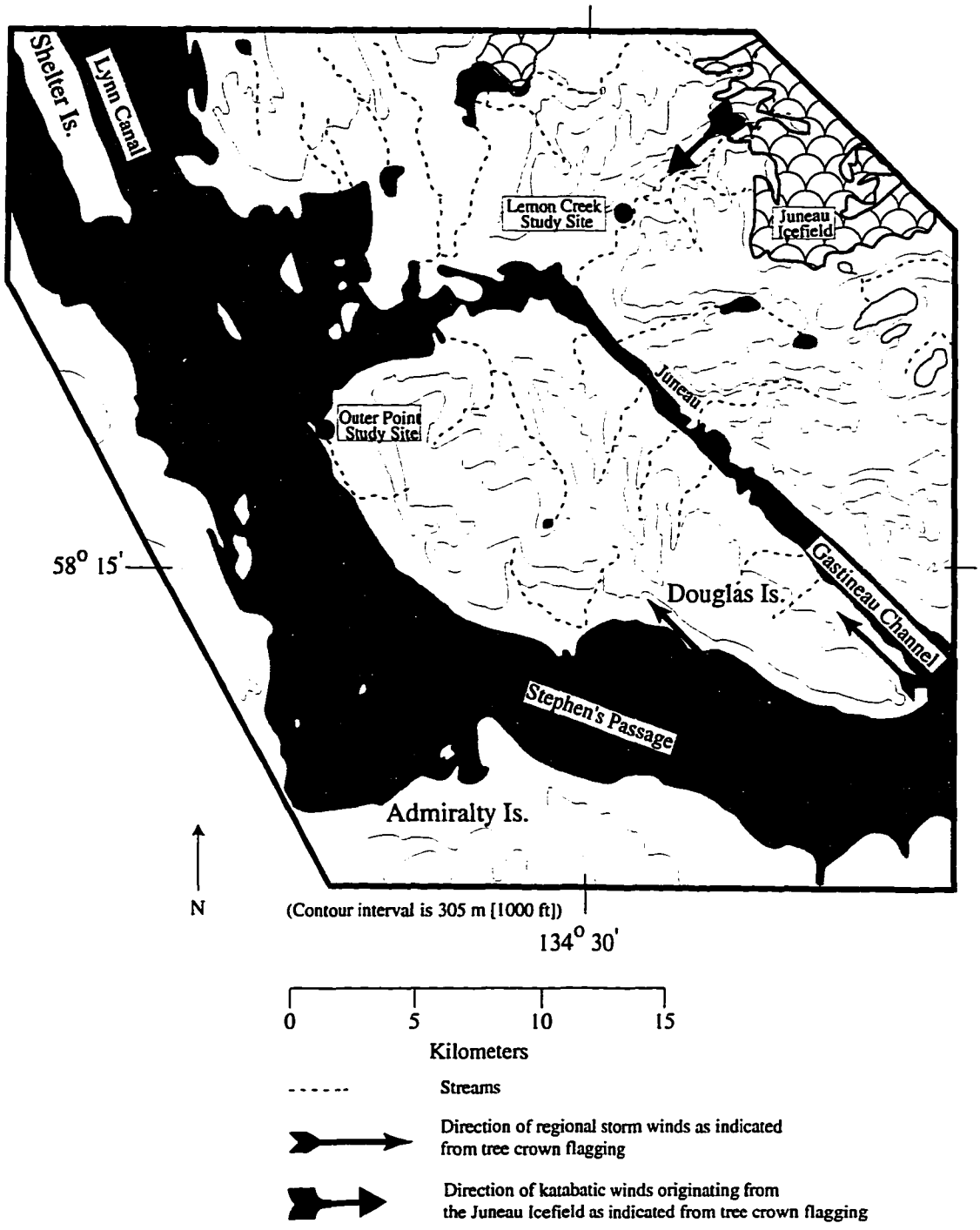


Figure 21. Locations of sites where interactions of individual treefalls, wind, and topography were investigated.

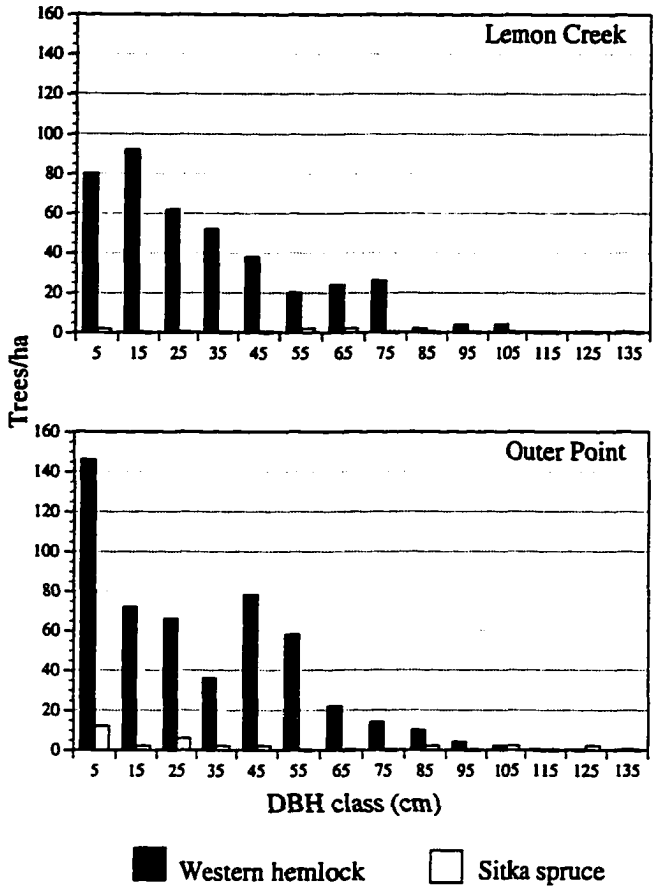


Figure 22. Frequency distributions of tree densities for site-level wind interpretation study sites. Tree densities are averages for five 0.1 ha reference plots at each site. The smallest size-class is 2.5-9.9 cm DBH; all other size-classes are 10 cm classes.

Northeast Chichagof Island.—A wind pattern map was constructed for northeast Chichagof Island in southeast Alaska. The mapped area consisted of the peninsula surrounded by Tenakee Inlet to the south, Chatham Strait to the east, and Port Frederick to the north (Figure 20).

The topography of the peninsula is complex, varying from mud flats exposed only at low tides to exposed rock surfaces in alpine areas. Elevation ranges from sea level to 1,191 m. Snow avalanche scars are common and often extend to valley bottoms because of the combination of steep slopes, fine textured soils, and abundant precipitation (J. Fincher, USDA Forest Service, pers. commun.).

Forest composition is dominated by Sitka spruce and western hemlock. Timber harvesting in the form of clearcutting has occurred in most watersheds on the peninsula.

METHODS

Site-Level Wind and Treefall Patterns

Site-level treefall direction data were collected from June through August, 1991-1993. Gapmaker data were collected as part of a study to describe small-scale natural disturbance regimes in southeast Alaskan forests (Chapter 2 of this thesis). A gapmaker is a tree whose death—or crown displacement in the case of leaning trees—results in the creation or expansion of a canopy gap (defined below). Gapmaker data relevant to this study were treefall direction and determination of whether the gapmaker fell downhill, uphill, or with slope contours. A tree was considered to have fallen downhill if treefall direction was within 45° in either direction of the aspect in the downhill direction. Similarly, a tree was considered to

have fallen uphill if treefall direction was within 45° in either direction of the aspect in the uphill direction. Gapmaker data were collected using the random, line intersect sampling design outlined by De Vries (1979). A sample line began at a boundary of a study site, passed through a pre-selected random point along a pre-selected random orientation, and ended when another boundary of the same study site was encountered. Detailed information about gapmakers was collected only in those gaps where the sample line crossed the long axis of the expanded gap. A gap could only be sampled once because random, line intersect sampling is a form of random sampling without replacement.

I defined a canopy gap as the land surface area directly under a canopy opening (Runkle 1982) that was formed from the death or displacement of a tree crown with an area equal to or exceeding the area occupied by an average codominant tree crown in the surrounding forest. The average width of the canopy gap along its long axis could not exceed the average total tree height of the surrounding forest (i.e. the ratio of average gap width along its long axis to average tree height of the surrounding forest is < 1). The average height of regenerating trees in the canopy gap could not exceed 50% of the average height of the surrounding forest canopy (i.e. the ratio of the average height of regeneration to average forest canopy height is < 0.5). This definition set minimum and maximum canopy gap areas and identified when the canopy of the tree regeneration in a gap merges with the surrounding forest canopy, thereby closing the gap.

An expanded gap consisted "of the canopy gap plus the adjacent area extending to the bases of canopy trees surrounding the canopy gap" (Runkle 1982).

A census of root-throws with a DBH > 2.5 cm was conducted on portions of the Outer Point and Lemon Creek study sites as part of a plant diversity assessment; a minimum of 50 root-throws was sampled at each site. Data collected for each root-throw that were relevant to this study were DBH, treefall direction, and a determination of whether a tree fell downhill, uphill, or with slope contours. It was necessary to identify root-throws as being either overstory or understory trees for conducting statistical analyses. I assumed that root-throws with DBHs greater than the minimum gapmaker DBH (24.0 cm at Outer Point, 25.0 cm at Lemon Creek) were overstory trees, with crown positions in the dominant/codominant canopy when they were alive. Root-throws with DBHs less than the minimum gapmaker DBH were assumed to be understory trees with subordinate canopy positions when they were alive.

Field observations of recent treefalls suggested that many trees had asymmetric crowns and that trees tended to fall with the heavy side (i.e. the side with the greatest crown volume) of their crown down. In order to test this observation, a survey of live crown asymmetry of trees in the dominant/codominant canopy layer was conducted. I was interested to see if treefall direction patterns corresponded with crown asymmetry patterns. A tree was considered to have an asymmetric crown if crown volume was noticeably concentrated on one side of a tree as determined by ocular estimation. The crown asymmetry survey was conducted using a modified random, line transect sampling approach. The starting point and orientation of a 3m-wide transect were determined in the same way as were the starting point and orientation of the random, line intersects outlined above. A sample transect began at a boundary of a study site, passed through a pre-selected

random point along a pre-selected random orientation, and ended when another boundary of the same study site was encountered. Trees in closed canopy forest— i.e. not canopy gap perimeter trees— were sampled if the centers of their root collars were located within a transect.

A perimeter tree is a tree whose crown helps define the boundary of a canopy opening. If one canopy gap perimeter tree was rooted within a transect, then all perimeter trees associated with the gap were sampled. This was done to ensure that perimeter trees from all sides of canopy gaps were represented. Sampled trees were recorded as either having symmetric or asymmetric tree crowns. The direction of tree crown asymmetry was the direction that the side of a tree crown with the greatest volume was facing.

Treefall and tree crown asymmetry directions are measured on circular scales. A circular scale is a special case of an interval scale where no true zero point exists and where any designation of values being low or high is arbitrary (Zar 1974). For example, there is no physical justification for assigning the direction of north a value of 0^{o} (or 360^{o}), and 90^{o} is not a "larger" direction than 60^{o} (Zar 1974).

Circular measurements are known in other disciplines in the natural sciences. For example, geologists examine glacial striations on rocks (Davis 1986) and biologists examine animal orientation and navigation (Batschelet 1981) using circular data analysis. Also, time periods on the scale of days, weeks, months, and years are circular (Zar 1974). Circular measurements such as treefall and wind directions are common in forest ecology, but statistical analyses other than calculation of a mean direction of these data are rarely performed. One notable exception was the work performed by Robertson (1987), who used circular data

analysis to help distinguish between purely biotic and abiotic processes as the primary cause of crown asymmetry in a balsam fir (*Abies balsamea*) wave forest.

Circular data analysis to investigate the relationship among treefall direction, aspect, and locally destructive wind directions, and between tree crown asymmetry and aspect. I will refer to the treefall direction data when describing the statistical procedures below, but the same techniques were used to investigate the relationship of tree crown asymmetry and aspect.

First, I determined if treefall direction was uniformly (i.e. randomly) distributed around a circle. I used the chi-squared goodness-of-fit test described by Batchelet (1981) for this purpose. The chi-squared test can be applied to circular data just as it is to linear data, with no adjustments. Also, this test is useful for both unimodal and multimodal populations, unlike some other tests of randomness that are only powerful when used with unimodal data (Batchelet 1981). The only restrictions are that data must be grouped so that the expected frequency in each group is ≥ 4, and the sample size should be at least 5 times the number of groups. The degree of freedom is the number of groups minus one (Batchelet 1981). I tested the null hypothesis that treefall direction was explained by a uniform frequency distribution about a circle. The alternative hypothesis was that treefall direction could not be explained by a uniform frequency distribution.

For those samples of treefall directions that were not uniformly distributed, I followed the procedures from Fisher (1993) to test the mean direction of treefall against a specified direction (i.e. destructive wind direction and/or aspect). This was done after I visually inspected the data sets to see that they were unimodally distributed.

Treefalls can be represented by vectors. Treefall vectors are unit vectors because they have a length equal to one.

Mean treefall direction.—Vector addition is the appropriate method to calculate the mean direction of a unimodal population of treefall vectors. An example will demonstrate why. Suppose 3 treefall directions are recorded as 0°, 45°, and 315°. It is apparent that the mean treefall direction will be 0° (or 360°). However, calculation of the arithmetic mean using $\sum_{i=1}^{n} \theta_i / n$, where θ_i represents direction of fall of an individual tree, will yield a value of 120°. If 0° is replaced with 360°, the arithmetic mean treefall direction is 240°. Obviously, the calculation of the arithmetic mean is not an appropriate method to calculate directional data because the same mean value is not always calculated from a sample. Also, the above mean values are obviously wrong since they lie outside the shortest arc distance separating the 3 treefall directions.

Individual treefall vectors were added by calculating

$$C = \sum_{i=1}^{n} \cos\theta_i, \qquad S = \sum_{i=1}^{n} \sin\theta_i \text{ (Fisher 1993)} \tag{1}$$

Then, the mean treefall direction $\overline{\theta}$ of the resultant vector of individual treefall vectors was determined by using the calculated values of C and S in the following contingency table:

$$\overline{\theta} = \begin{cases} \tan^{-1}(S/C) & \text{when } S>0,\ C>0 \\ \tan^{-1}(S/C)+\pi & \text{when } C<0 \\ \tan^{-1}(S/C)+2\pi & \text{when } S<0,\ C>0 \end{cases} \text{ (Fisher 1993)} \tag{2}$$

The length of the resultant vector is represented by R and was calculated from

$$R = \sqrt{C^2 + S^2} \text{ (Fisher 1993)} \tag{3}$$

R has a value in the range of 0 to n. The mean resultant vector length $\overline{R}$ associated with mean treefall direction $\overline{\theta}$, was calculated using

$$\overline{R} = R / n \text{ (Fisher 1993)} \quad (4)$$

$\overline{R}$ has a value in the range of 0 to 1.

Sample circular dispersion.—Sample circular dispersion was used to calculate a confidence interval of mean treefall direction at a study site. Sample circular dispersion was calculated as

$$\hat{\delta} = (1 - \hat{\rho}_2) / (2\overline{R}^2) \text{ (Fisher 1993)} \quad (5)$$

where

$$\hat{\rho}_2 = (1/n)\sum_{i=1}^{n} \cos 2(\theta_i - \overline{\theta}) \text{ (Fisher 1993)} \quad (6)$$

Nonparametric estimation of a confidence interval of mean treefall direction.—The mean value of a population parameter is designated μ, where the population consists of all individuals about which inferences are to be made. The mean value of a sample within a population is $\hat{\mu}$. In the case of treefall directions, the point estimate of $\hat{\mu}$ is $\overline{\theta}$ and can be calculated using equation 2. Calculation of an interval estimate (e.g. 95% confidence interval) for μ is dependent upon sample size. It should be noted that the sample or sub-sample of interest must be distributed unimodally in order to perform the following calculations.

When the treefall sample size was < 25, a 95% confidence interval for μ was obtained using bootstrap methods. The bootstrap program was written to allow for a sample that was drawn from a non-symmetric distribution (Fisher 1993). The confidence interval was determined from 200 bootstrap samples.

When treefall sample size was ≥ 25, I calculated a 95% confidence interval for μ using a set of equations. First, I calculated the circular dispersion $\hat{\delta}$ using equation 5. Then the circular standard error $\hat{\sigma}$ of $\hat{\mu}$ was calculated from

$$\hat{\sigma} = \sqrt{\hat{\delta} / n} \text{ (Fisher 1993)} \quad (7)$$

Finally, an approximate $100(1-\alpha)\%$ confidence interval for μ was calculated from

$$(\hat{\mu} - \sin^{-1}(z_{1/2\alpha}\hat{\sigma}), \quad \hat{\mu} + \sin^{-1}(z_{1/2\alpha}\hat{\sigma})) \text{ (Fisher 1993)} \quad (8)$$

where $z_{1/2\alpha}$ is the upper $100(1/2\alpha)\%$ point of a standard normal distribution and where $\alpha = 0.05$.

Testing a mean treefall direction for a specified value.—I tested the hypothesis that the mean direction of treefalls μ of a study site was not significantly different from a specified direction such as wind direction or aspect μ_0. In other words, I wished to test the null hypothesis that $\mu = \mu_0$ against the alternative hypothesis that $\mu \neq \mu_0$, at the $\alpha = 0.05$ level of significance. Because the 95% confidence interval for μ was already calculated, the only remaining step was to check whether or not μ_0 was within the interval. If μ_0 lay within the confidence interval, I accepted the null hypothesis at the 95% level, otherwise I accepted the alternative hypothesis (Fisher 1993).

Landscape-Level Wind Flows and Blowdown Patterns

I constructed a landscape-level wind pattern map for northeast Chichagof Island during the summers of 1993 and 1994. Landscape-level wind patterns were interpreted from:

1) Low elevation (<450 m) tree crown flagging,

2) Treefalls in large-scale blowdowns—both recent and historic, and

3) Treefalls adjacent to clearcuts.

Low elevation tree crowns were flagged as a result of mechanical damage, but they were not flagged to the extent commonly associated with krummholz trees. The mechanical damage responsible for flagging suggests that this damage is caused by strong winds. Storm winds usually occur during the fall and winter months in southeast Alaska (Harris 1989). Western hemlock exhibited flagging to a much greater extent than Sitka spruce. Evidence of wind direction from tree crown flagging was obtained from a helicopter.

Recent large-scale blowdowns were those in which treefall direction could be determined from a helicopter. Direction of treefall in recent large-scale blowdowns and of blowdowns adjacent to clearcuts was obtained at the same time tree crown flagging information was obtained.

Historic blowdowns were those that required ground reconnaissance to determine treefall direction. These blowdowns were previously identified from aerial photographs by the USDA Forest Service, Tongass National Forest, Chatham Area.

RESULTS

Site-Level Wind and Treefall Patterns

Outer Point study site.—Tree crown flagging indicated that storm winds are from the southeast (Figure 21). Therefore, I tested the null hypothesis that mean treefall direction was equal to 315°. The Outer Point study site does not have an appreciable slope, so treefall direction was not compared to aspect.

Gapmaker treefall directions were not uniformly distributed at Outer Point (Figure 23A, $x^2 = 22.4$, df = 6, $P < 0.001$). The mean direction of gapmaker treefall (291°) was not significantly different from the direction of storm winds (Figure 23A).

Root-throw treefall direction patterns at Outer Point were dependent upon tree size. Overstory trees that were root-thrown were not uniformly distributed (Figure 24A, $x^2 = 50.13$, df = 10, $P < 0.001$). The mean direction of treefall of overstory root-throws (317°) was not significantly different from the direction in which southeast gale winds blow. Smaller diameter understory root-throws were uniformly distributed (Figure 24B, $x^2 = 5.92$, df = 4, $0.199 < P < 0.287$).

Crown asymmetry was observed in 40.5% (n = 45) of the 111 sampled crowns of trees in closed canopy forest at Outer Point. Asymmetric crowns of trees in closed canopy forest were not uniformly distributed (Figure 25A, $x^2 = 26$, df = 8, P = 0.001). The mean direction of the sides of crowns with the greatest volume was 200°.

The proportion of asymmetric tree crowns was greater in the sample of canopy gap perimeter trees. Crown asymmetry was observed in 70.8% (n = 63) of the 89 sampled canopy gap perimeter trees. Asymmetric live crowns of perimeter trees, however, were uniformly distributed at Outer Point (Figure 25B, $x^2 = 7.65$, df = 11, $0.713 < P < 0.799$). The vast majority (96.8%) of asymmetric perimeter tree crowns were directed toward their respective gaps.

Lemon Creek study site.—Tree crown flagging indicated that destructive winds at the Lemon Creek site are glacier winds that originate over the Juneau Icefield and not southeast gales (Figure 21). Average aspect of the site is 112°.

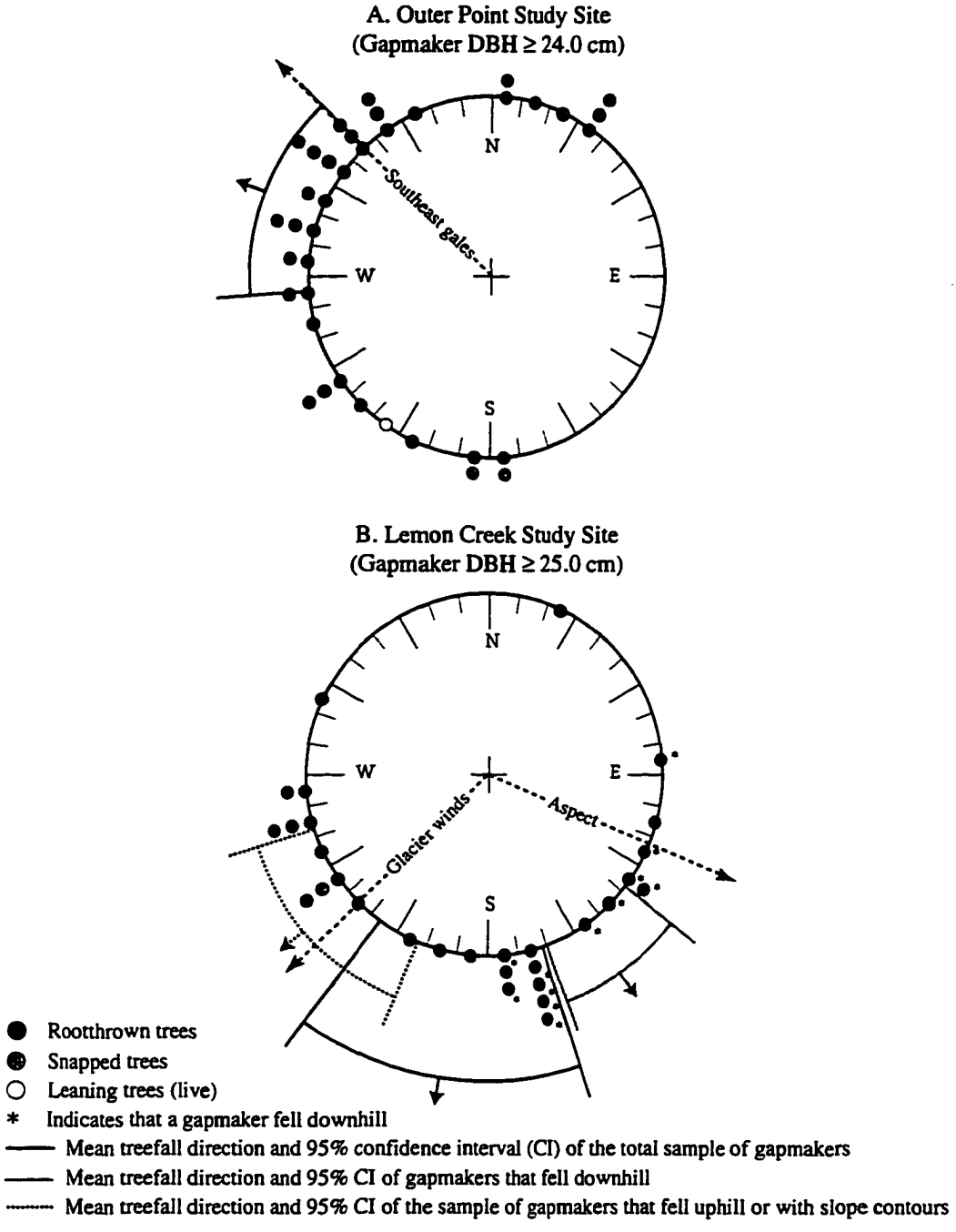


Figure 23. Gapmaker treefall directions at Outer Point and Lemon Creek. Each dot represents one tree. Treefall directions were actually recorded to the nearest degree.

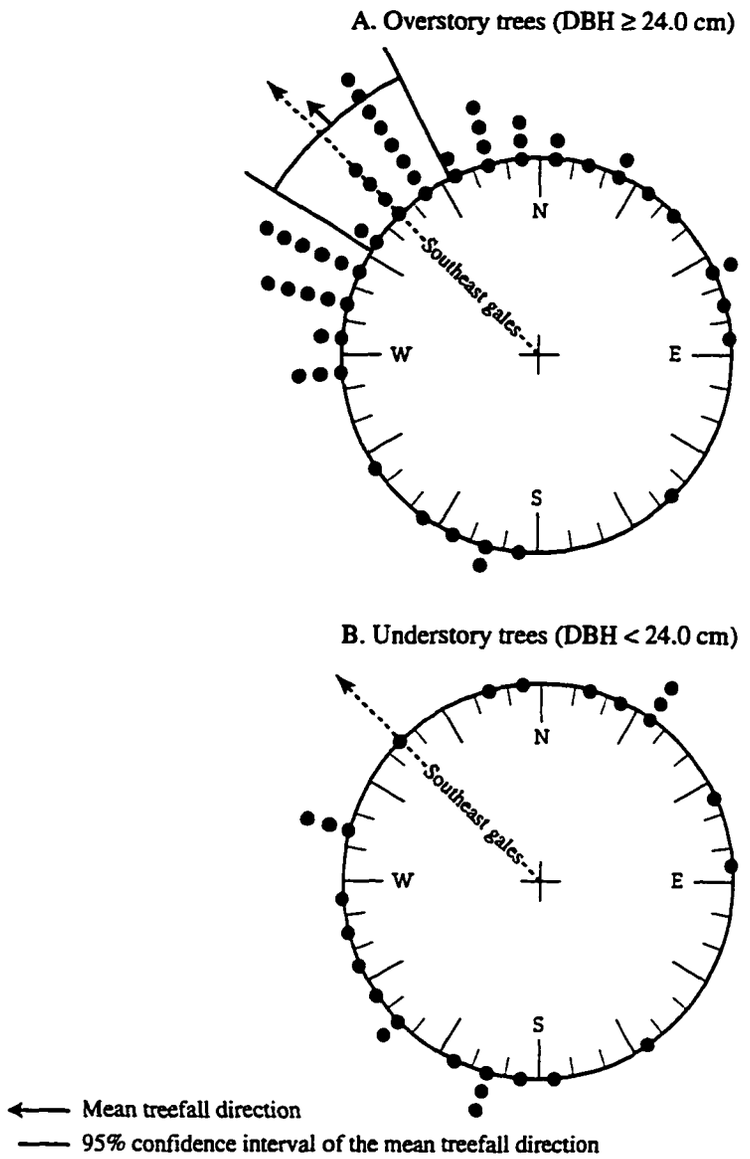


Figure 24. Treefall directions of root-throws at the Outer Point study site. Minimum tree diameter was 2.5 cm. It was assumed that root-throws with DBHs ≥ 24.0 cm (minimum gapmaker DBH) were trees with dominant or codominant crown positions (i.e. overstory trees) when alive. Root-throws with DBHs < 24.0 cm were assumed to be trees with subordinate canopy positions (i.e. understory trees) when they were alive. Each dot represents one tree. Treefall directions were actually recorded to the nearest degree.

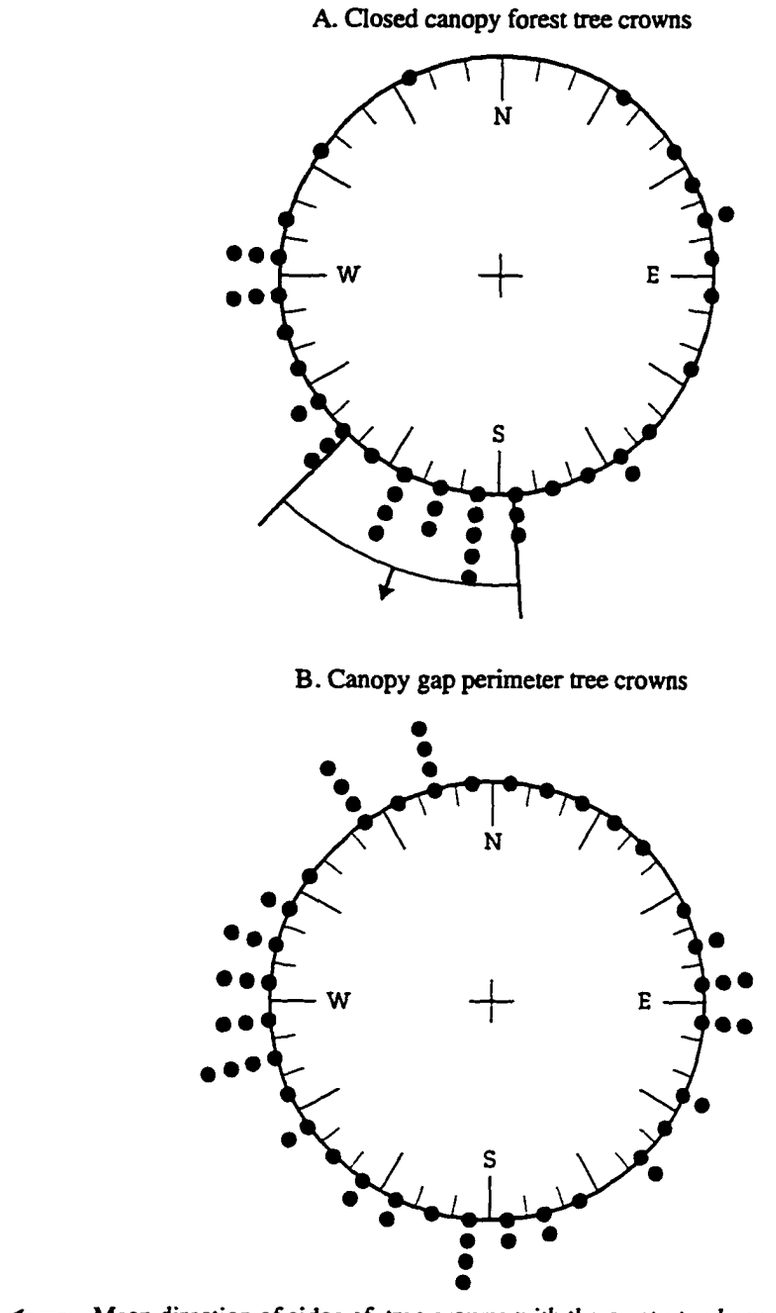


Figure 25. Directions of asymmetric tree crowns at the Outer Point study site. Asymmetry was recorded as the direction in which the side of a live crown with the greatest volume was facing. Only trees with dominant and codominant crowns positions were measured. Each dot represents one tree.

Therefore, I tested the null hypothesis that mean treefall direction was equal to 225° (direction of flow of glacier winds) and 112°.

Treefall directions for all gapmakers were not uniformly distributed at Lemon Creek (Figure 23B, $x^2 = 20.4$, df = 5, $P < 0.001$). The mean direction of treefall of all sampled gapmakers (190°), and the 95% confidence interval lie between the direction of flow of glacier winds and the aspect of the site.

However, mean treefall direction was different for 2 objectively defined sub-populations of gapmakers that had unimodal distributions at Lemon Creek. One sub-population of gapmakers fell downhill; the other sub-population of gapmakers included all other trees—those that fell uphill or with slope contours (Figure 23B). The mean treefall direction (145°) and the 95% confidence interval for gapmakers that fell downhill were between the direction of the aspect and direction of flow of glacier winds (Figure 26). Mean treefall direction of the gapmakers that fell uphill or with the contour was 230°. The direction of flow of glacier winds fell within the 95% confidence interval for the mean treefall direction of this sub-population. The 95% confidence intervals of mean treefall direction of both sub-populations of gapmakers at Lemon Creek did not include the direction of flow of southeast gales.

Root-throw treefall direction patterns at Lemon Creek were dependent upon tree size. Overstory trees that were root-thrown had a treefall distribution pattern similar to the distribution of gapmakers at this site. The distribution of treefall directions of the entire population of overstory root-thrown trees was not uniform (Figure 26A, $x^2 = 15.06$, df = 5, $0.007 < P < 0.010$). Mean treefall direction (180°) and the 95% confidence interval of mean treefall direction of the entire sample of

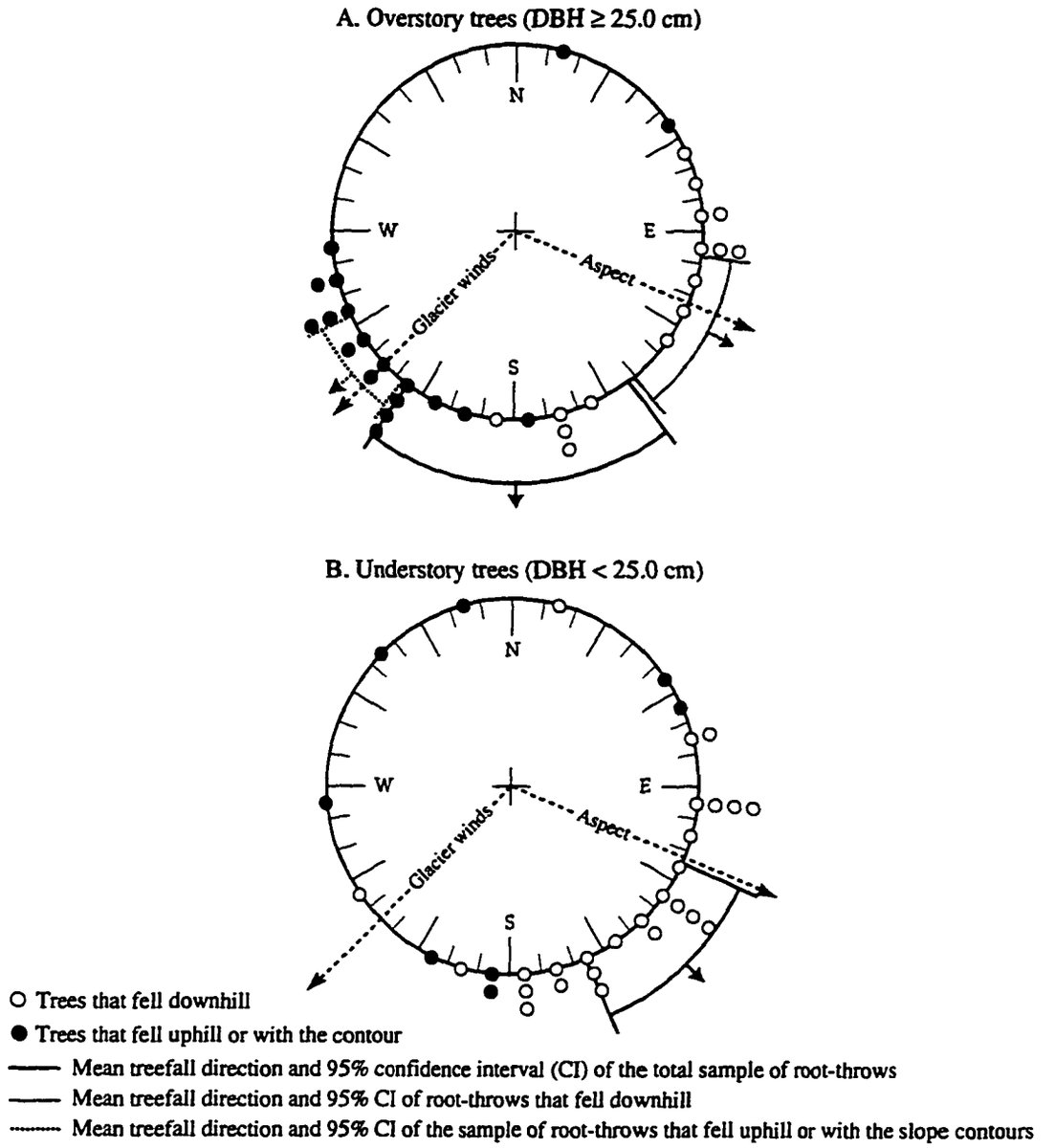


Figure 26. Treefall directions of root-throws at the Lemon Creek study site. Minimum tree diameter was 2.5 cm. It was assumed that root-throws with DBHs ≥ 25.0 cm (minimum gapmaker DBH) were trees with dominant or codominant crown positions (i.e. overstory trees) when alive. Root-throws with DBHs < 25.0 cm were assumed to be trees with subordinate canopy positions (i.e. understory trees) when they were alive. Each dot represents one tree. Treefall directions were actually recorded to the nearest degree.

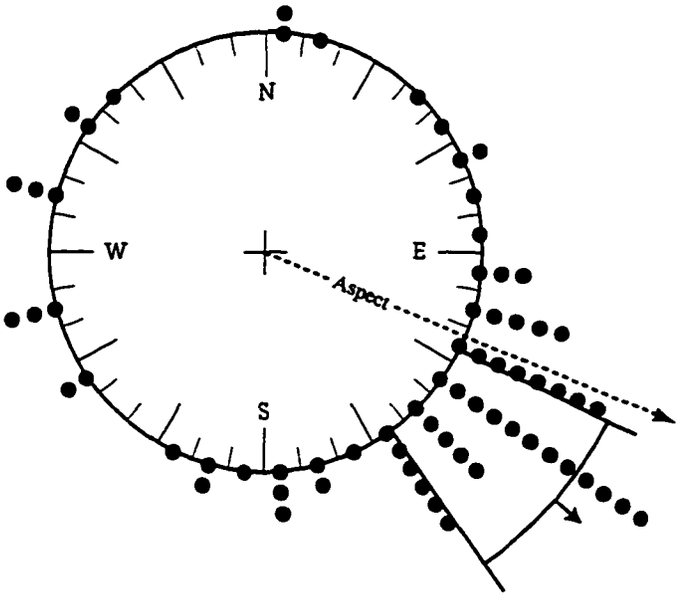
overstory root-throws lie between the direction of the aspect and the flow of glacier winds (Figure 26A).

Mean treefall direction was different for 2 objectively defined sub-populations of root-throws of overstory trees that had unimodal distributions at Lemon Creek. Mean treefall direction of the sub-population of overstory root-throws that fell downhill was 117°, and the 95% confidence interval included the direction of the aspect, but not the direction of flow of glacier winds or southeast gales (Figure 26A). Also, the majority of root-throws of overstory trees that fell downhill did not fall on the downwind side of the direction of the aspect. Mean treefall direction of the sub-population of root-throws of overstory trees that did not fall downhill was 229°; the 95% confidence interval included the direction of flow of glacier winds (Figure 26A).

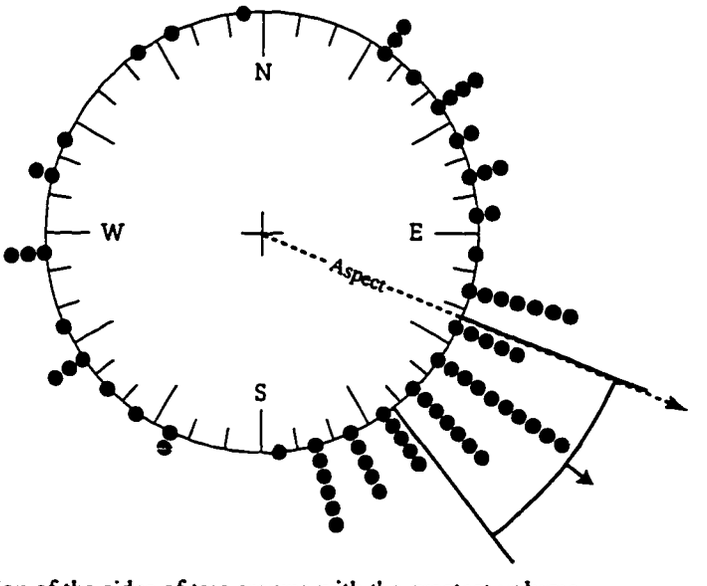
Treefall directions of understory root-throws at Lemon Creek were not uniformly distributed (Figure 26B, $x^2 = 26.0$, df = 5, $P < 0.001$). The mean treefall direction of the entire sample of understory root-throws was 135°. The 95% confidence interval of mean treefall direction lies between the direction of the aspect and the direction of flow of glacier winds, but it is much closer to the direction of the aspect. Of these understory root-throws, 76.5% fell downhill. Understory root-throws were not analyzed as sub-populations of trees that fell downhill or as trees that fell uphill or with slope contours.

The directionality of the sides of dominant and codominant tree crowns with the greatest volume in closed canopy forest at Lemon Creek was not uniformly distributed (Figure 27A, $x^2 = 87.02$, df = 11, $P < 0.002$). Crown asymmetry was observed in 67.6% (n = 69) of the 102 sampled crowns of trees in closed canopy

A. Closed canopy forest tree crowns



B. Canopy gap perimeter tree crowns



⟵ Mean direction of the sides of tree crowns with the greatest volume

—— 95% confidence interval of the mean direction

Figure 27. Directions of asymmetric tree crowns at the Lemon Creek study site. Asymmetry was recorded as the direction in which the side of a live crown with the greatest volume was facing. Only trees with dominant and codominant crowns positions were measured. Each dot represents one tree.

forest at Lemon Creek; of these, 68.1% were asymmetric downhill. The mean direction of the sides of crowns with the greatest volume was 130°.

The directionality of the sides of tree crowns with the greatest volume was not uniformly distributed for canopy gap perimeter trees (Figure 27B, $x^2 = 68.23$, df = 11, $P < 0.002$). Crown asymmetry was observed in 78.2% (n = 79) of the 101 sampled crowns of perimeter trees at Lemon Creek. Of these asymmetric perimeter tree crowns, 49.4% were asymmetric into their respective gaps, 65.8% were asymmetric downhill, and 31.6% were asymmetric into gaps as well as downhill. Note that these values are not mutually exclusive.

Landscape-Level Wind Flows and Blowdown Patterns

Evidence of wind direction on northeast Chichagof Island obtained from tree crown flagging, treefalls in large-scale blowdowns, and treefalls adjacent to clearcuts was used to construct landscape-level wind flow maps. Two maps were constructed because wind flows across the peninsula are concentrated in both a northward direction (Figure 28, see map pocket) and a southward direction (Figure 29, see map pocket). Tree crown flagging and treefall directions that could be interpreted as being a result of either a northward-flowing or southward-flowing wind were included on both maps.

There were 43 large-scale natural blowdowns—recent and historic—associated with northward-flowing winds (Figure 28). These blowdowns were concentrated at the tip of the peninsula south of Freshwater Bay (n = 9, 20.9%), and in the Indian River drainage west of the southern most tip of the peninsula (n = 7, 16.3%). Large-scale natural blowdowns associated with northward-flowing winds were also

concentrated northwest of the Vortex (n = 6, 14.0%). Thirty blowdowns adjacent to clearcuts were associated with northward-flowing winds (Figure 28). These blowdowns were concentrated in the northeast portion of the peninsula north of Freshwater Bay (n = 19, 63.3%).

There were 24 large-scale natural blowdowns and 14 blowdowns adjacent to clearcuts associated with southward-flowing winds (Figure 29). These blowdowns were not concentrated in particular portions of the landscape. The number of blowdowns, both natural and those adjacent to clearcuts, associated with southward-flowing winds was only 52% of the number of blowdowns associated with northward-flowing winds.

DISCUSSION

Site-Level Wind and Treefall Patterns

The relationship between treefall direction and the direction of flow of destructive winds varied with tree size and topography. The direction of fall of trees that were previously growing in the overstory, such as gapmakers and large diameter root-throws (a subset of gapmakers), can be indicative of the direction of flow of destructive winds. However, care must be taken when inferring wind flow from treefall directions on steep slopes. Treefall directions of small diameter understory trees did not correspond to known wind flows.

The finding that only overstory trees were indicative of destructive wind flows is not surprising. Larger tree crowns have greater forces exerted on them by wind, and the turning moment increases with the length of the lever arm (i.e. tree height)

as trees become taller (Harris 1989). Also, understory trees are subjected to slower wind velocities than overstory trees (Kittredge 1948).

Treefall directions of overstory root-throws and gapmakers in general were similar at each site. At Outer Point, a mostly level site, treefall direction patterns suggest that southeast gales are the primary disturbance agent. The direction of average treefall for both sample populations was not significantly different than the direction of flow of southeast gales. The same relationship between treefall direction and southeast gales was observed in a riparian Sitka spruce forest with a negligible slope on Douglas Island (unpubl. data).

Crown asymmetry patterns apparently do not control treefall direction patterns at Outer Point. Crown asymmetry appears to be a response of trees to light availability. The direction of asymmetric tree crown growth in closed canopy forest was variable, but was concentrated in the direction of the path of the sun (southwest) and perpendicular to the direction of flow of southeast gales. Asymmetric tree crowns around canopy gaps faced into the gaps. Growth rates of branches would presumably be greater on the sides of trees facing canopy gaps because light levels would be greater within the gaps. Trees would not be expected to fall preferentially with their heavy sides down in this forest.

Treefall direction patterns of gapmakers and overstory root-throws are more complex at Lemon Creek, a site with a steep slope. Treefall patterns suggest that glacier winds cause some treefalls while other treefalls result from disturbance agents that cause trees to fall downhill, possibly without the influence of wind. The Lemon Creek site is apparently sheltered from southeast gales.

When all gapmakers or overstory root-throws are viewed, mean direction of treefall appears to result from an interaction of glacier winds and slope effects. Glacier winds cause the treefalls and the trees rotate in a downhill direction as they fall.

Analysis of the sub-populations of gapmakers and overstory root-throws allows for a more critical evaluation of treefall dynamics. Glacier winds appear to be the cause of trees that fell uphill or with slope contours. Treefalls that occurred downhill may have resulted from glacier winds or an interaction of glacier winds and slope. However, they may also have resulted from other causes such as snow-loading or gravitational forces acting on trees that were leaning downhill due to soil creep. These results oppose those of Alexander and Buell (1955) who determined that all classes of trees (e.g. alive, dead, root-thrown, snags) in a forest located in the Rocky Mountains of Colorado fell in the direction of prevailing winds, uninfluenced by topography.

Like Outer Point, crown asymmetry patterns appear to be a response to light availability at Lemon Creek. But unlike Outer Point, crown asymmetry may influence treefall direction patterns at Lemon Creek. Tree crown asymmetry at this site appears to be influenced by slope. Downhill sides of trees receive more sunlight, resulting in greater crown volume on the downhill sides. Slope effects on crown asymmetry are apparently greater than the effect of canopy gaps. Overstory trees at Lemon Creek are always under the influence of slope effects on the light environment. However, the effects of canopy gaps on the light environment are transitory because gaps infill and eventually disappear. Crown asymmetry appears to have influenced treefall directions of the sub-populations of gapmakers and

overstory root-throws that fell downhill; those trees would have tended to fall with their heavy sides down. The sub-population of gapmakers and overstory root-throws that are indicative of the direction of flow of glacier winds probably did not fall with their heavy sides down.

Landscape-Level Wind Flows and Blowdown Patterns

Wind flows across northeast Chichagof Island are very complex. In general, wind is funneled into low elevation areas by the surrounding steep-walled topography.

Northward-flowing winds.—The dominant topographic features of the peninsula are valleys, coastlines, and mountains oriented along a southeast to northwest axis. Northward-flowing winds originating south of the peninsula and blowing north through Chatham Strait are deflected by steep topography into the valleys and along parallel coastlines (Figure 28).

Several areas of turbulence are notable. Air flow over Iyoukeen Peninsula results in turbulent airflow to its north. This wind pattern is most apparent if the wind flow arrows from Maps 1 and 2 are viewed together. Simultaneous wind flow around the north and south sides of the large karst feature known locally as the Vortex results in turbulence at its northwest end. Treefall directions in a large historic blowdown at the northwest end of the Vortex indicate wind flows from 2 directions. The distribution of treefalls that were created when the current stand was initiated was bimodal, with mean treefall directions being northwest (315°) and south-southwest (201°). It appears that a turbulence pocket also exists at the mouth of Iyouktug Creek that drains into False Bay. Water in the bay swirls in a

counterclockwise direction when winds blow from the south. Also, treefall direction patterns in forest stands located on level ground in the mouth of the Iyouktug drainage do not indicate a dominant wind direction. However, the presence of historic large-scale natural blowdowns on the north side of the drainage indicates that strong winds from the south do enter the drainage. If a turbulence pocket did not exist at the mouth of the Iyouktug drainage, treefall direction patterns would be expected to indicate a north- or northwest-flowing wind.

Winds flowing northward across northeast Chichagof Island are most likely associated with low pressure cells that originate in the Gulf of Alaska. Southeast gales are the most common and most damaging fall and winter storms in southeast Alaska. During the period 1953-78, the frequency of winds > 30 mph that originated from the southeast (east-southeast to south-southeast) was 81.6% at Annette Island, 94.7% at Juneau, and 85.8% at Yakutat (Harris 1989).

Large-scale natural blowdowns were concentrated at the tip of the peninsula south of Freshwater Bay and in the Indian River drainage. These areas are the first places where southeast gales blowing north through Chatham Strait would interact with the land mass of northeast Chichagof Island. Large-scale natural blowdowns were also concentrated northwest of the Vortex. It is likely that the venturi effect is created in the narrow valley on the north side of the Vortex. Increased wind velocity resulting from the venturi effect would make destructive winds from southeast gales even more destructive in the valley northwest of the Vortex.

The concentration of blowdowns adjacent to clearcuts in the northeast portion of the peninsula may be the result of a northwest deflection of strong winds, made even stronger by the venturi effect, into False Bay and Iyouktug Creek. The shape

of the coastline of the northeast portion of the study site (north of Iyoukeen Peninsula) results in a narrowing of Chatham Strait (Figure 210). It is likely that the venturi effect is created in this narrowing. Strong south winds blowing north through Chatham Strait would be made stronger because of the venturi effect.

The concentration of large-scale natural blowdowns and blowdowns adjacent to clearcuts in certain portions of northeast Chichagof Island suggests that some areas of the peninsula are more prone to wind disturbance than others. Areas deemed most prone to wind disturbance from this project appear to be the tip of the peninsula south of Freshwater Bay, the Indian River drainage, the Game Creek watershed northwest of the Vortex, and the northeast portion of the peninsula. The spatial distribution of a more complete analysis of large-scale natural blowdowns (USDA Forest Service, Tongass National Forest, Chatham Area, unpubl. data) generally supports these observations.

Southward-flowing winds.—Southward-flowing winds originate north of northeast Chichagof Island, and flow across the peninsula in a southerly direction along Chatham Strait and Port Frederick and through the numerous interior valleys that are generally oriented north to south (Figure 29). Southward-flowing winds appear to flow over higher elevation saddles and ridges in the mountains with a southeast to northwest orientation.

Southward-flowing winds are most likely associated with high pressure cells having a clockwise rotation that develop in the Gulf of Alaska. Southward-flowing winds could also be glacier winds that originate in the icefields in Glacier Bay National Park to the north and in the Coast Mountains on the mainland to the northeast. However, storm winds from the north are rare. Of all winds > 30 mph

from 1953-78, winds from the north (northeast to northwest) comprised 1.3% at Annette Island, 0.4% at Juneau, and 0.7% at Yakutat (Harris 1989). Another indication that the most damaging winds on this landscape are from the south is the fact that about half as many blowdowns were associated with southward-flowing winds compared to northward-flowing winds.

Management Implications

Understanding landscape-level wind flows across a landscape can provide insights into which portions of that landscape are most prone to stand-level disturbances and which portions are relatively protected from destructive wind flows. This information can be used to make decisions regarding which silvicultural system would be most appropriate to use on different portions of a landscape. I have demonstrated the feasibility of mapping wind patterns across large, forested, complex landscapes. Acquiring the information necessary to construct a wind pattern map for 120,000 ha landscape can be accomplished in about 6 hours of flight time.

Understanding site-level wind flows can provide insights into how to shape and orient harvest units, and where to place harvest unit boundaries with the intent of minimizing wind damage to the surrounding forest. Information about site-level wind flows can be obtained from treefall directions of large-scale blowdowns, tree crown flagging, and treefall directions of small-scale disturbance events such as canopy gaps.

Care should be used when inferring wind direction from populations of individual treefall directions. Only the direction of fall of trees that were

previously growing in the overstory (i.e. dominant and codominant crown positions) should be used. Care should also be used to account for potential topographic influences on treefall direction in steep terrain. Circular data analysis techniques are useful when inferring wind direction from individual treefall directions.

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CHAPTER 4

SYNTHESIS

INTRODUCTION

Wind is the primary natural disturbance agent of southeast Alaskan forests; it causes disturbance at a variety of scales and intensities. Most of southeast Alaska lies within the boundaries of the Tongass National Forest and is managed by the USDA Forest Service. Forest managers in the region are very aware of wind disturbance, especially at larger scales. Wind storms can result in stand-level blowdown events and cause damage along clearcut edges created by timber harvest. Also, there is recognition that high frequency, low intensity disturbance events (i.e. canopy gaps) are common on the landscape.

Other than salvaging timber blown down during wind storms, the recognition that wind is the major disturbance agent to forests in southeast Alaska has not traditionally been a major factor in forest management activities in the region. However, there has been a shift in the approach to natural resource management in recent years. All federal resource management agencies are now in the process of defining and/or implementing ecosystem management in some form. With the advent of ecosystem management there has been an increased demand by the Forest Service for additional information about wind and its effects on southeast Alaskan forests.

My research described in this thesis focused on 3 issues relating to natural disturbance in southeast Alaskan forests. My primary focus was on: (1) characterizing some aspects of small-scale natural disturbance regimes and their

variability, and (2) determining the effects of small-scale disturbances on the understory light environment and some aspects of forest structure and composition. The third aspect of my research dealt with identifying methods that enabled me to interpret wind and treefall patterns at the site- and landscape-levels in forests of southeast Alaska.

GAP DYNAMICS

Natural disturbances are major forces that shape ecosystems and landscape patterns. These disturbances provide the context within which long-term management strategies to sustain desired conditions of ecosystem diversity and productivity must be developed (Salwasser and Pfister 1994). It has been suggested that information about the natural range of variability of ecosystems can be used as a guide for ecosystem management. Natural variability can be characterized by the range of ecosystem conditions such as the extent of particular seral classes of vegetation and by the disturbance regime. Swanson et al. (1994) suggested that managing an ecosystem within its range of natural variability was appropriate for maintaining diverse, resilient, productive, and healthy ecosystems. A key premise to this approach is that native species have adapted to, and in part, evolved with the natural disturbance events of the Holocene environment. Accordingly, the potential of survival of native species is reduced if their environment is pushed outside the range of its natural variability (Swanson et al. 1994).

Disturbances resulting from wind in southeast Alaskan forests can be broadly categorized as being small-scale, resulting from the death of 1 or several trees, or large-scale, stand-level events. Presumably, native species in the region have adapted

to, and evolved with disturbances at both scales. My research focused on characterizing small-scale natural disturbances (i.e. gaps) for 3 sites, with structural features of old-growth, in the western hemlock (*Tsuga heterophylla*)/blueberry (*Vaccinium spp.*)/shield fern (*Dryopteris austriaca*) forest plant association in northern southeast Alaska. This plant association is common on the landscape and is important for timber production, wildlife habitat, and esthetics.

Canopy gaps (all ages) comprised about 9% of the forest area; expanded gaps comprised about 27% of the forest area at the 3 sites. Gap and gapmaker characteristics generally were similar among sites. The majority of canopy gaps were < 50 m^2 in area, had a D/H ratio < 0.50; were created from the death of 1 or 2 gapmakers; and had experienced gap expansion. The majority of expanded gaps were < 200 m^2. Gapmakers were usually snapped and concentrated in younger decay classes.

Understanding specific effects of natural disturbance on a forest system requires not only knowledge of the physical characteristics of the disturbance of interest, but also knowledge of the response of the forest to the disturbance. For the same 3 sites where I described gap characteristics, I also described the influence of canopy gaps on:

1) The understory diffuse light environment,

2) Plant species richness and cover,

3) Woody vegetation height, and

4) Tree regeneration.

Light levels were greatest and most variable in canopy gaps at both the shrub and herb layers. Both point sample and gap-level light values generally decreased, and

were less variable, along the gradient from canopy gap to transition gap to closed canopy forest. Light interception by shrub layer plants resulted in a decrease in light levels at the herb layer. This relationship, however, was highly variable.

No significant relationships were found between plant species richness and gap area or between species richness and light levels at the scale of 1 m^2. Plant cover was not associated with light levels at the scale of 1 m^2 either. The only significant relationships that were identified were between plant species (or group of species) cover expressed as a % of the total area of a gap that was sampled (gap-level species cover) and mean light intensity at the gap level (canopy or transition gap). However, these relationships were not consistent among sites, species, or positive/negative nature of the relationships.

No significant correlations were found between light levels at the shrub layer and the height of the tallest individual of each woody species rooted in the 1 m^2 understory vegetation plots. However, some relationships existed between the mean and median heights of woody species and forest position. Mean and median heights of western hemlock at all sites were largest in canopy gaps and smallest under closed canopy forests. This trend existed for some of the other woody species at some sites, but it was not consistent.

Sitka spruce appears to have the potential to maintain itself through gap-phase replacement only at one of the 3 sites. This site has the largest mean and median gap areas and highest diffuse shrub light levels of the 3 sites. It is generally accepted that Sitka spruce requires relatively large-scale disturbances because of its higher light requirements compared to western hemlock. The ability of spruce to maintain itself in a stand through gap-phase dynamics appears to be marginal at best.

Results of this research project do not indicate a consistent influence of gaps on forest understory dynamics. Results of other studies, however, have demonstrated the effects of gaps (e.g. Runkle 1990, Spies et al. 1990). The lack of consistent relationships between gaps and forest understory characteristics is probably indicative of the data collection limitations of this study.

The significance of gaps in forest dynamics can only be appreciated by considering larger spatial scales and including the temporal nature of gap dynamics. Gaps occur in the old-growth stage of forest development described by Oliver (1981). Oliver's model of forest development following a stand-replacing disturbance is accepted by the Forest Service in southeast Alaska (Iverson et al. 1996). According to this model, a forest that is initiated following a stand-replacing disturbance goes through 4 stages of development in the absence of additional major disturbances. The stand initiation stage represents the time during which new seedlings become established on a site, and sprouting stems and advance regeneration begin or resume growth. The stem exclusion stage represents the time during which new tree establishment is excluded and vertical stratification by species occurs in the existing stems because of intense competition for resources. The stem exclusion stage usually begins upon canopy closure in light-limited forests. The understory reinitiation stage is the period when herbaceous and woody plants, including advance regeneration, begin to grow in the understory as the overstory becomes very mature. The old growth stage is the final stage of development when the overstory slowly breaks up (i.e. gaps are formed) and understory advance regeneration is locally released and moves into the overstory canopy.

By limiting the scope of this project to old-growth forests, more significant effects of canopy gaps were probably masked. Gaps comprise part of the fabric of old-growth forests. It is their creation that allows the development of structural and species diversity in the understory of a forest stand that was previously depauperate of both forms of diversity in the middle stages of forest development.

Treating gaps as discrete entities probably also resulted in the lack of consistent relationships among gaps, light, and forest understory vegetation. The effect of gaps on forest dynamics is probably cumulative. A particular point in the understory of a forest can be under the influence of several gaps simultaneously, especially in high latitude forests with a high degree of sidelighting. Gap density and spatial arrangement may have a greater influence than individual gap size on understory forest dynamics.

The variables measured during this study may have been inappropriate to detect consistent relationships among gaps and understory light and vegetation. For example, plant biomass or seedling densities may be better variables than leaf cover estimated in 10% increments for detecting those relationships.

Finally, information about gap age may be important for understanding relationships between forest overstory and understory dynamics. For example, seedling density in Douglas-fir (*Pseudotsuga menziesii*) forests was found to correlate with gap age but not gap size (Spies et al. 1990). I was unable to reliably determine gap age because vegetation in a gap was sometimes responding to more than one disturbance.

EMULATING NATURAL DISTURBANCE REGIMES

Current timber management practices have characteristics of both large-scale and small-scale natural disturbance regimes. Small-scale natural disturbances occur frequently but at a low intensity whereas large-scale natural disturbances occur infrequently but at high intensity. The human-caused disturbance regime represented by the clearcut silvicultural system is both high frequency—current rotation ages of 90 to 120 years (DeGange 1996) do not produce stands beyond the stem exclusion stage—and high intensity.

There are potential problems with the clearcut silvicultural system as currently applied. Organisms in the region are not adapted to the combination of high frequency and high intensity disturbance events on a landscape (and regional) scale. The potential exists for reduced biological diversity in second growth stands over successive rotations (Hill 1979) because of limited dispersal capabilities of some plant species (Alaback and Herman 1988, Matlack 1994).

Current timber management practices have characteristics of both large-scale and small-scale natural disturbances in another way. Snapped trees, accompanied by little soil disturbance, characterize the most common mode of tree death in small-scale natural disturbances. Root-thrown trees, accompanied by much soil disturbance to the lower depths of tree rooting at a given site, characterize the most common mode of tree death in large-scale natural disturbances (pers. observ.). Clearcutting results in large-scale disturbances with relatively little soil disturbance at more than superficial depths.

Removal of trees through harvest emulates tree mortality of small-scale wind disturbances more closely than those of large-scale wind disturbances, because cut

trees are similar to the majority of gapmakers (snapped) in the sense that both forms of tree mortality lack displacement of the rootwad and the associated soil disturbance.

Harvesting second growth stands at current rotation ages will decrease the number of trees with large root systems because second growth stands are harvested before the trees reach the large sizes characteristic of the older stages of forest development (i.e. understory reinitiation and old-growth stages). This reduction in the number of large, root-thrown trees potentially will reduce the functional contribution of large rootwads to soil disturbance. For example, podzolization of soil may result in the development of a placic soil horizon that is relatively impermeable, thereby hindering drainage of the overlying soil and resulting in paludification (degeneration to acidic muskeg) of the site (Ugolini and Mann 1979). Large root-throws may make a critical contribution to site productivity through soil churning that may increase site drainage (Lawrence 1958).

Small-scale natural disturbances that occur in second growth stands at current rotation ages may result in a greater proportion of root-thrown trees compared to that observed in older forests. Younger trees are less likely to snap compared to older trees because they have less internal decay characteristic of older trees. Therefore, younger trees in second growth stands are expected to root-throw more often than older trees in forests in the understory reinitiation stage and old-growth stage. However, the root-thrown trees in the second growth stands have smaller root systems compared to older, larger root-thrown trees in older forests. The result may be proportionally more root-thrown trees in second growth stands, but these trees may result in formation of rootwads that are smaller, shallower, and less functional in terms of soil disturbance than those in older forests. The overall rate of canopy

gap formation is expected to be less in second growth stands compared to older forests, even though the proportion of root-thrown trees may be greater. The rationale for this statement is that second growth stands at current rotation ages will not achieve an age where trees are as susceptible to wind damage as trees in stands that are in the understory reinitiation and old-growth stages of development.

Emulating natural wind disturbance regimes in forests of southeast Alaska will require addressing human-caused disturbances at both the large and small scales. As already mentioned, timber management as it currently exists demonstrates attributes of both scales of natural disturbance.

Emulating the large-scale natural disturbance regime would require lengthening the rotation ages of clearcuts to allow second growth stands to achieve an age where they develop characteristics of the understory reinitiation and old-growth stages of forest development. Sitka spruce regenerates primarily through large-scale disturbance events. Therefore, large-scale disturbances of human origin, with longer rotation ages and possibly more size variation, are consistent with the paradigm of managing forests within the range of natural variability, both temporally and spatially.

Emulating natural disturbance regimes would require the addition of small scale timber harvest activities to mimic canopy gaps. Emulating the small-scale natural disturbance regime probably would be best achieved if single tree selection and small group selection cuts were administered within a stand. Decision rules to determine how many trees to remove to create an "artificial gap", and where and when to remove additional trees during stand re-entries can be developed from characteristics of natural canopy gaps.

Forest management activity that simulates small-scale natural disturbance may result in a reduced incidence of fluted western hemlock, thereby increasing the quality of this tree species on the managed landscape. Fluted trees have buttressed root collars and vertically oriented furrows (flutes) that spiral up the trunk (Julin et al. 1993). Fluted logs are difficult to debark for pulp and usable volume is reduced (Julin et al. 1993). Some of the factors leading to severe hemlock fluting are:

1) Growth in even-aged stands that develop following large-scale natural disturbances and clearcuts;

2) Codominant and dominant crown positions; and

3) Large, persistent branches (Julin et al. 1993).

All of these factors suggest that fast growing western hemlock trees in high light environments are the most prone to severe fluting. In fact, Julin et al. (1993) found that flute initiation was strongly correlated with the time at which trees showed accelerated diameter growth.

A persistent alder (*Alnus sinuata*) brush stage often develops in portions of clearcuts where soil is highly disturbed. Dense thickets of alder can slow tree seedling growth (Fastie 1994). Creation of "artificial gaps" similar in size to natural canopy gaps may reduce the incidence of the alder brush stage in harvest units. Alder is light-demanding species (Viereck and Little 1986), so the low light levels found in small gaps would probably minimize successful establishment of this shrub, even when soil is disturbed.

UNDERSTANDING WIND FLOWS

The third aspect of this research project dealt with identifying methods that enabled me to interpret wind and treefall patterns at the site- and landscape-levels in forests of southeast Alaska. Application of ecosystem management concepts to an actual landscape will require knowledge of wind flows—and intensities—in order to assess the risk of wind damage to forests at both the site- and landscape-levels.

Understanding landscape-level wind flows, especially of destructive winds, across a landscape can provide insights into which portions of that landscape are most prone to stand-level disturbances and which portions are relatively protected from destructive wind flows. This information can be used to make decisions regarding which silvicultural system would be most appropriate to use on different portions of a landscape. Understanding site-level wind flows can provide insights into how to shape and orient harvest units, and where to place harvest unit boundaries with the intent of minimizing wind damage to the surrounding forest.

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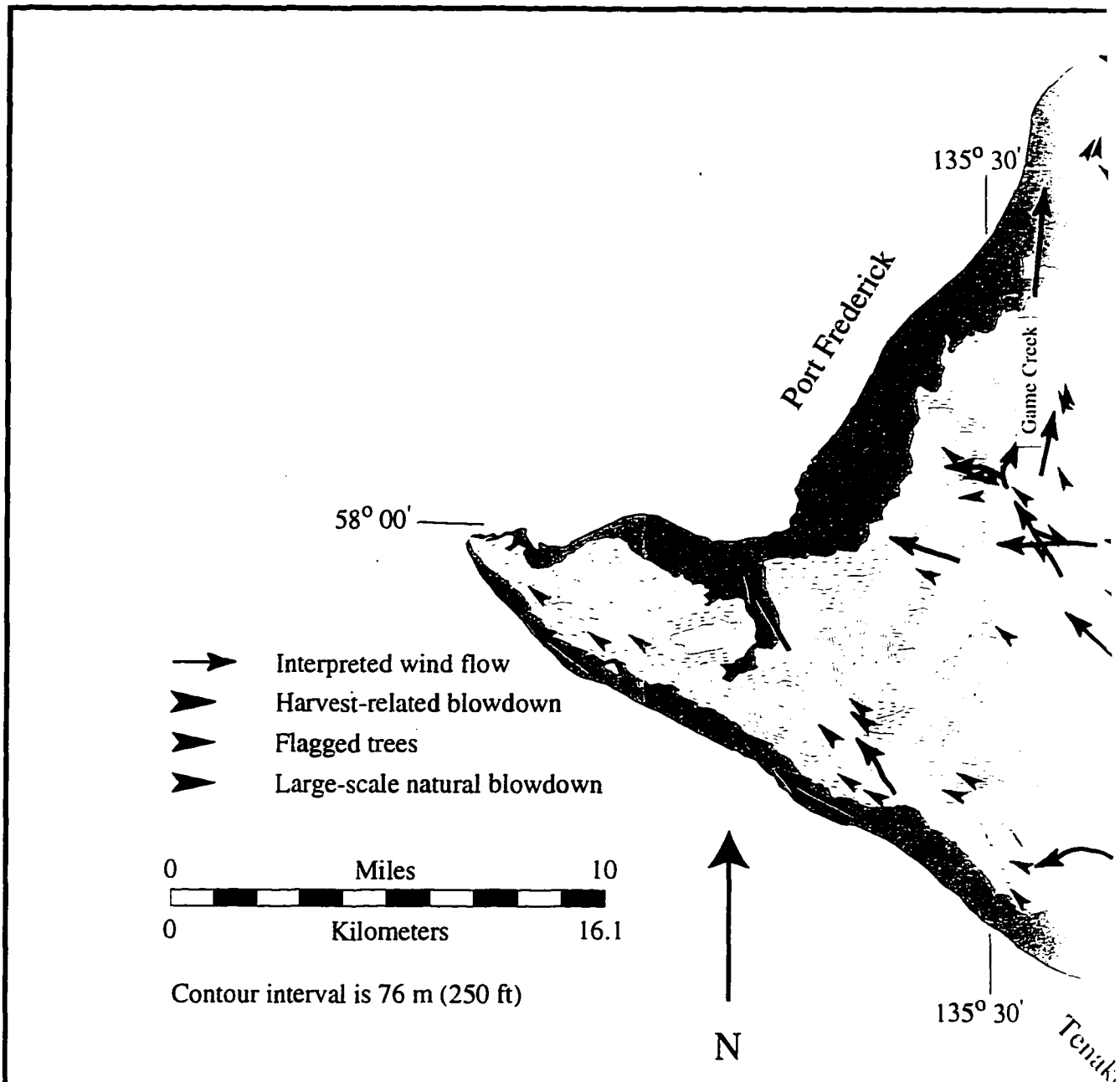
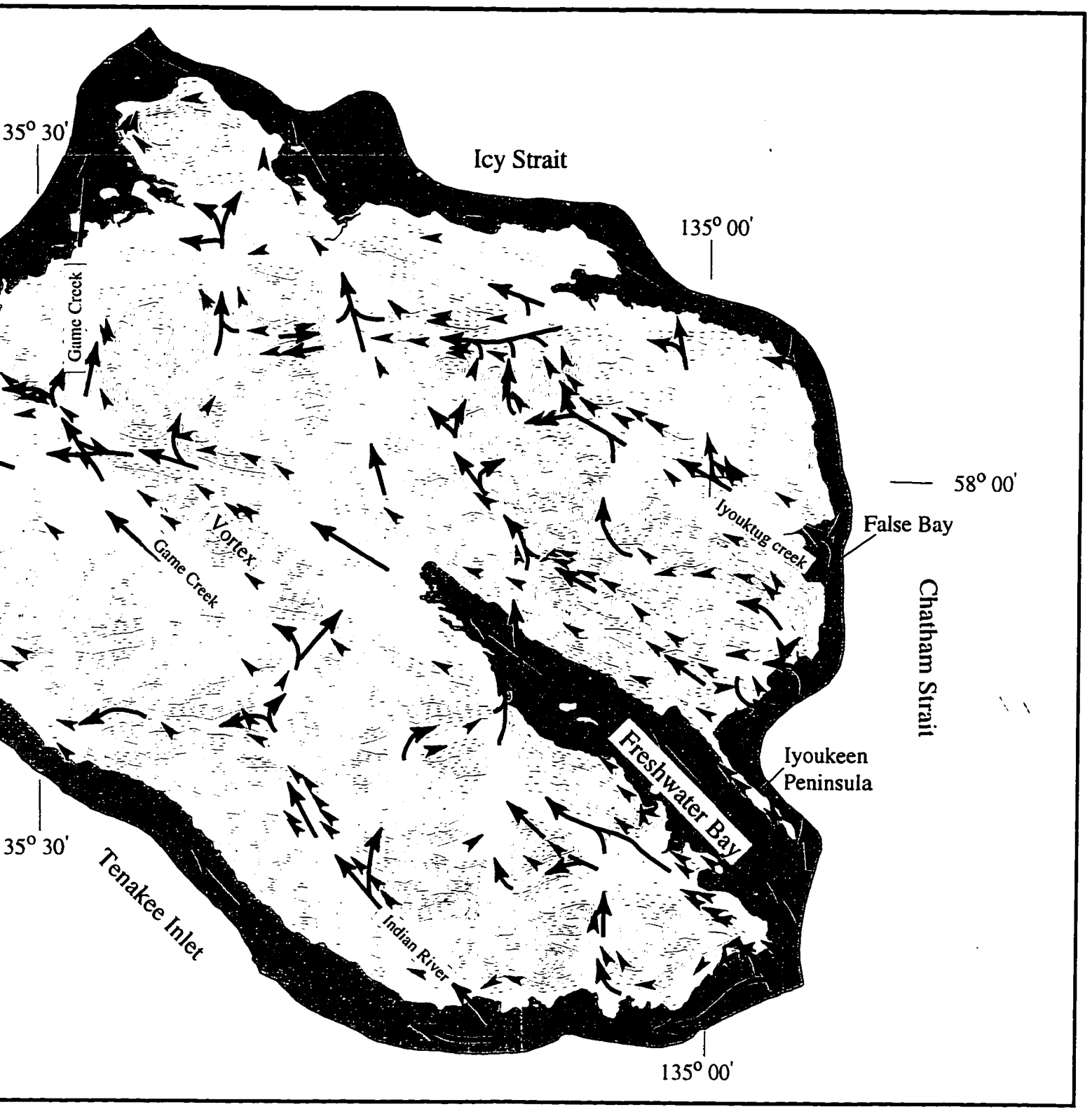


Figure 28. Interpreted north-flowing winds across northeast Chichagof Island



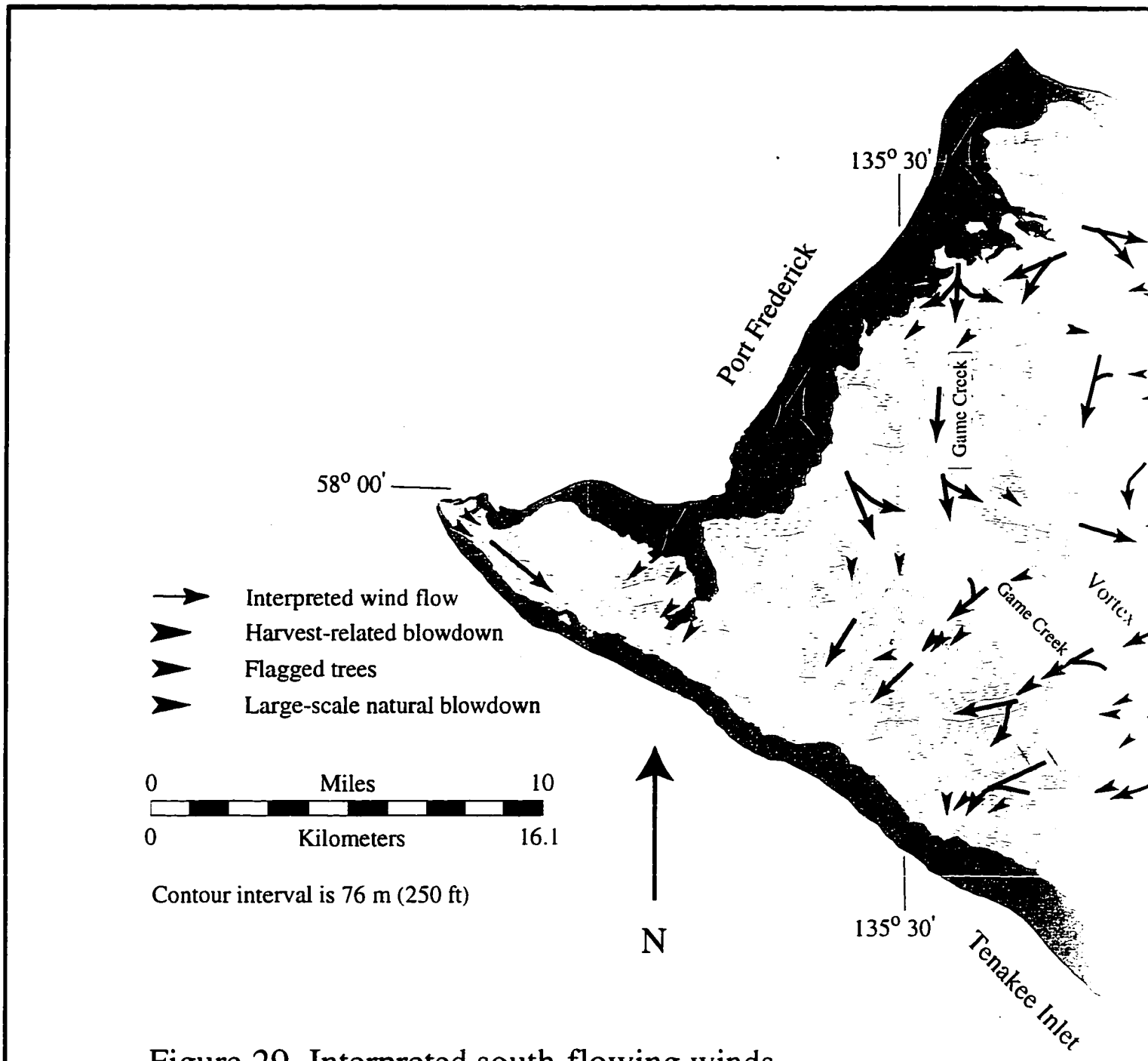


Figure 29. Interpreted south-flowing winds across northeast Chichagof Island